Fishery Bulletin

Vol. 84, No. 4 October 1986

POLOVINA, JEFFERY J., and STEPHEN RALSTON. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas.. 759

YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, W. H. HULET, and R. T. HANLON. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle 771

BODKIN, JAMES LEE. Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests of central California 799

STEPIEN, CAROL A. Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard, 1854 809

PAULY, DANIEL. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments 827

FINUCANE, JOHN H., L. ALAN COLLINS, HAROLD A. BRUSHER, and CARL H. SALOMAN. Reproductive biology of king mackerel, *Scomberomorus cavalla*, from the southeastern United States 841

FARLEY, C. A., S. V. OTTO, and C. L. REINISCH. New occurrence of epizootic sarcoma in Chesapeake Bay soft shell clams, *Mya arenaria* 851

FOLKVORD, ARILD, and JOHN R. HUNTER. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes 859

SMITH, JOSEPH W., and JOHN V. MERRINER. Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay 871

McGOWAN, MICHAEL F. Northern anchovy, *Engraulis mordax*, spawning in San Francisco Bay, California, 1978-79, relative to hydrography and zooplankton prey of adults and larvae 879

HUNTER, J. ROE, BEVERLY J. MACEWICZ, and JOHN R. SIBERT. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific 895

HOUDE, EDWARD D., and LAWRENCE LUBBERS III. Survival and growth of striped bass, *Morone saxatilis*, and *Morone* hybrid larvae: laboratory and pond enclosure experiments 905

DAILEY, MURRAY D., and STEPHEN RALSTON. Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp, *Heterocarpus laevigatus*, in Hawaii 915

RALSTON, STEPHEN. An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago 927

DITTY, JAMES G. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality 935

(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

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CONTENTS

Vol. 84, No. 4 October 1986

POLOVINA, JEFFERY J., and STEPHEN RALSTON. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas.. 759
YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, W. H. HULET, and R. T. HANLON. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle 771
BODKIN, JAMES LEE. Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests of central California 799
STEPIEN, CAROL A. Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard, 1854 809
PAULY, DANIEL. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments 827
FINUCANE, JOHN H., L. ALAN COLLINS, HAROLD A. BRUSHER, and CARL H. SALOMAN. Reproductive biology of king mackerel, *Scomberomorus cavalla*, from the southeastern United States 841
FARLEY, C. A., S. V. OTTO, and C. L. REINISCH. New occurrence of epizootic sarcoma in Chesapeake Bay soft shell clams, *Mya arenaria* 851
FOLKVORD, ARILD, and JOHN R. HUNTER. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes 859
SMITH, JOSEPH W., and JOHN V. MERRINER. Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay 871
McGOWAN, MICHAEL F. Northern anchovy, *Engraulis mordax*, spawning in San Francisco Bay, California, 1978-79, relative to hydrography and zooplankton prey of adults and larvae 879
HUNTER, J. ROE, BEVERLY J. MACEWICZ, and JOHN R. SIBERT. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific 895
HOUDE, EDWARD D., and LAWRENCE LUBBERS III. Survival and growth of striped bass, *Morone saxatilis*, and *Morone* hybrid larvae: laboratory and pond enclosure experiments 905
DAILEY, MURRAY D., and STEPHEN RALSTON. Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp, *Heterocarpus laevigatus*, in Hawaii 915
RALSTON, STEPHEN. An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago 927
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(Continued on next page)

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REXSTAD, ERIC A., and ELLEN K. PIKITCH. Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus* 947
PEREZ, MICHAEL A., and MICHAEL A. BIGG. Diet of northern fur seals, *Callorhinus ursinus*, off western North America 957
TESTER, PATRICIA A., and ANDREW G. CAREY, JR. Instar identification and life history aspects of juvenile deepwater spider crabs, *Chionoecetes tanneri* Rathbun ... 973

Notes

CODY, TERRY J., and BILLY E. FULS. Comparison of catches in 4.3 m and 12.2 m shrimp trawls in the Gulf of Mexico 981
POWELL, ALLYN B., and GERMANO PHONLOR. Early life history of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus* 991
PODNIESINSKI, GREG S., and BERNARD J. McALICE. Seasonality of blue mussel, *Mytilus edulis* L., larvae in the Damariscotta River estuary, Maine, 1969-77 995

Index 1003

Notices 1017

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AN APPROACH TO YIELD ASSESSMENT FOR UNEXPLOITED RESOURCES WITH APPLICATION TO THE DEEP SLOPE FISHES OF THE MARIANAS

JEFFREY J. POLOVINA AND STEPHEN RALSTON[1]

ABSTRACT

A comprehensive approach to estimate the maximum sustainable yield (MSY) for a tropical multispecies resource which lacks catch and effort data is presented. This yield assessment approach was used to design a fishery resource assessment survey of the Mariana Archipelago. An application of the method is presented to estimate the MSY for a multispecies bottom fish resource, based on data collected during the survey. The annual MSY for the deep slope fishes (primarily snappers and groupers) of the Mariana Archipelago is estimated to be 109 t, which for comparative purposes is equivalent to 222 kg/nmi of 200 m isobath or 0.3 t/km^2.

Assessment of tropical resources has always created major problems in fisheries research (Saila and Roedel 1979; Pauly and Murphy 1982). This has been largely due to three factors: technical difficulties in aging, a high species diversity in tropical communities, and what is typically a multiplicity of artisanal gears used in these fisheries. The latter problem has been especially difficult to surmount, making it difficult to determine not only the level of fishing effort but sometimes even the total catch. Without these data many standard fisheries techniques such as stock-production methods are inapplicable (but see Csirke and Caddy 1983).

In recent years, however, new methods and modifications of existing methods have been proposed to estimate growth and mortality parameters, standing crop, and yield for fish stocks in the absence of a time series of commercial catch and effort data (Beddington and Cooke 1983; Pauly 1983; Polovina 1986a; Wetherall et al. in press). We will show that several of these techniques can be combined, producing an integrated approach to yield assessment designed specifically for tropical fisheries resources in situations where catch and effort data are lacking. The approach is then applied to data gathered in a fishery survey of the Mariana Archipelago to estimate maximum sustainable yield (MSY) for a multispecies resource of deep slope snappers and groupers.

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YIELD ASSESSMENT

The equilibrium yield assessment is presented schematically in Figure 1. This approach assumes that growth follows the deterministic von Bertalanffy curve with parameters K and L_∞, that the mortality of fish above the smallest length fully represented in the catch (L_c) occurs at a constant instantaneous rate (Z), and that recruitment is constant with R recruits entering the first vulnerable age class annually. It is also assumed that the resource is essentially pristine, such that an estimate of the biomass recruited to the fishery in the absence of exploitation (B_∞) can be obtained from a catch-per-unit-effort (CPUE) survey and an estimate of catchability. In the discussion section, the effect of relaxing some of these assumptions will be considered.

For each species under consideration, the data required for this program, at a minimum, consist of a large length-frequency sample, otolith data and/or a time series of length-frequency data, a systematic CPUE survey, and an estimate of catchability, such as that obtained from an intensive fishing experiment. The large length-frequency sample is used to jointly estimate the asymptotic length (L_∞) and the ratio of total instantaneous mortality (Z) to the von Bertalanffy growth parameter (K) based on the following relationship:

$$\Theta = Z/K = (L_\infty - \bar{l})/(\bar{l} - L_c),$$

where L_c is a parameter defined above and $\bar{l}$ is the mean length of all fish greater than L_c (Beverton

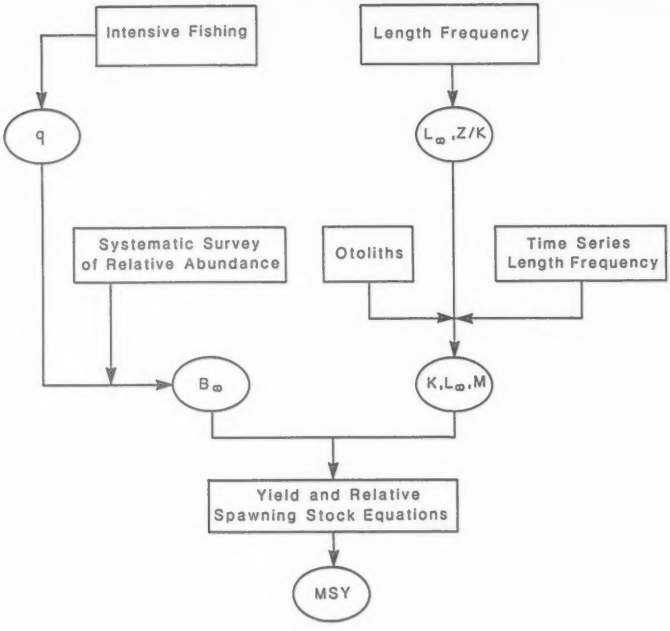

FIGURE 1.—Schematic of the yield assessment approach. A more general approach to fishery assessment which includes a treatment of catch and effort data as well is given in Munro (1983); our Figure 1 represents a detailed subset of Munro's figure 1 (1983).

and Holt 1956). For a series of L_c values at intervals beginning with the smallest L_c and going up to L_∞, there will be a corresponding set of $\bar{l}$ values. By solving the Z/K equation above for $\bar{l}$ as a function of L_c, the following relationship is obtained:

$$\bar{l} = L_\infty/(\Theta + 1) + L_c\,(\Theta/(\Theta + 1)).$$

Thus, regressing a sequence of $\bar{l}$ values on the corresponding L_c values will produce estimates for the slope and intercept which can be solved for estimates of L_∞ and Z/K (Wetherall et al. in press).

Once an estimate of L_∞ has been obtained by this method, otolith data and/or a time series of length-frequency data can be fit to the von Bertalanffy growth curve to estimate the growth coefficient K. Estimation of L_∞ from length-frequency data was used for the Marianas bottom fish data because a large length-frequency sample was available and otolith readings were difficult to interpret for old stages of growth. With an estimate for K, the total mortality rate, Z, can then be estimated as the product of K and the ratio of Z/K obtained in the previous step. Alternatively, one can estimate Z from a catch curve constructed from a length-frequency sample which has been corrected for nonlinear growth and converted to an age-frequency sample (Pauly 1983).

If these techniques are applied to unexploited or lightly exploited resources, the estimate of Z provides an estimate of the instantaneous rate of natural mortality (M). However, if fishing mortality is believed significant, an equation to estimate M as a function of K, L_∞, and mean annual water temperature (T) (in °C) has been developed as follows (Pauly 1983):

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} \mathrm{T}.$$

Given estimates of K, M, and age of entry to the fishery (t_c), the Beverton and Holt (1957) yield per recruit (Y/R) equation can be used to compute the ratio of equilibrium yield to unexploited recruited biomass as a function of fishing mortality (F). The

equilibrium yield (Y) can be expressed as

$$Y = R F \int_{t_c}^{\infty} \exp(-tM - (t - t_c) F)\, w(t)\, dt,$$

where $w(t) = W_\infty (1 - \exp(-Kt))^b$, and where W_∞ is the asymptotic weight and b is the exponent of the length-weight relationship. The unexploited recruited biomass (B_∞) can be expressed as

$$B_\infty = R \int_{t_c}^{\infty} w(t) \exp(-Mt)\, dt.$$

The ratio of equilibrium yield to unexploited recruited biomass (Y/B_∞) is then independent of W_∞ and R, depending only on K, M, t_c, F, and b. Tables and computational formulae are readily available to evaluate these integrals for Y and B_∞ as functions of t_c and F (Beverton and Holt 1966; Beddington and Cooke 1983). Upon estimation of B_∞, the equilibrium yield is estimated for a given level of F as the product of Y/B_∞ and B_∞.

If a stock is unfished, B_∞ can be estimated by mapping the relative abundance of the stock in terms of CPUE from a systematic survey and then converting estimates of relative abundance into biomass with an estimate of catchability. There are a number of methods which have been used to estimate catchability (Ricker 1975). For work on Pacific island fishery resources, an intensive fishing approach, which fishes a small isolated location heavily and regresses CPUE on cumulative catch (Leslie model), has been used successfully to estimate catchability for bottom fishes and shrimp (Polovina 1986a; Ralston 1986). If only one estimate of catchability is obtained, then the standing stock per unit of area is determined as the ratio of CPUE to catchability in the appropriate units of weight or numbers. If several estimates of catchability are available corresponding to different levels of CPUE, then it might be appropriate to fit a more general power function relationship between CPUE and standing stock (Bannerot and Austin 1983).

The product of Y/B_∞ and B_∞ as a function of F is the equilibrium yield based on the assumption of constant recruitment. While this assumption will be valid for low levels of exploitation, there will come a point as F increases that recruitment will begin to decline and sustainable yield may thus be less than the yield predicted under the assumption of constant recruitment. Estimating MSY yield as the maximum equilibrium yield obtained over all F from the product of Y/B_∞ and B_∞ may, therefore, overestimate the actual MSY. There are two adjustments which have been proposed to estimate MSY in the absence of detailed knowledge of the spawner-recruit relationship. One approach is to estimate MSY from the constant recruitment yield curve as that yield corresponding to that level of F where the addition of one unit of mortality increases the yield by 10% of the amount caught by the first unit of F (Gulland 1983, 1984). This level of mortality and corresponding yield have been denoted as $F_{0.1}$ and $Y_{0.1}$, respectively. A second approach to estimating MSY from the constant recruitment yield curve is to use the Beverton and Holt equation to calculate the ratio of the spawning stock biomass under exploitation (S) to the spawning stock biomass in the absence of exploitation (S_0) and to use this ratio as an indicator of the sustainability of a yield for a given combination of F and t_c. For simplicity, we assume that the age of sexual maturity (t_m) is identical for both sexes. Then the unexploited spawning stock biomass (S_0) is

$$S_0 = R \int_{t_m}^{\infty} \exp(-Mt)\, w(t)\, dt,$$

and

$$S = R \int_{t_m}^{\infty} \exp(-Mt - (t - t_c) F)\, w(t)\, dt.$$

Thus, the ratio of S/S_0 depends only on M, K, t_c, t_m, and F.

It has been suggested that the spawning stock biomass of a species should not be reduced below 20% of its unexploited level if a substantial reduction in the recruitment is to be avoided (Beddington and Cooke 1983). Thus, the estimate of MSY is determined as the maximum yield from the constant recruitment curve subject to the constraint that F does not exceed the level which reduces the relative spawning stock biomass below 0.20 of S_0.

ASSESSMENT OF SNAPPERS AND GROUPERS IN THE MARIANAS

The Mariana Archipelago consists of a chain of islands and banks on a north-south axis beginning with Galvez Banks and Santa Rosa Reef at the southern end and extending northward to Farallon de Pajaros (30 nmi north of Maug Island). A chain of seamounts also runs on a north-south axis

about 120 nmi west of the high island chain (Fig. 2).

Six resource assessment cruises of 40 d each were conducted in the Marianas during the period from May 1982 through June 1984. During these cruises, the deepwater snapper and grouper community along the outer slope was sampled at all 22 islands and banks labeled in Figure 2. Thirteen of these 22 sampling sites were visited at least once during the first three cruises and, again, during the second set

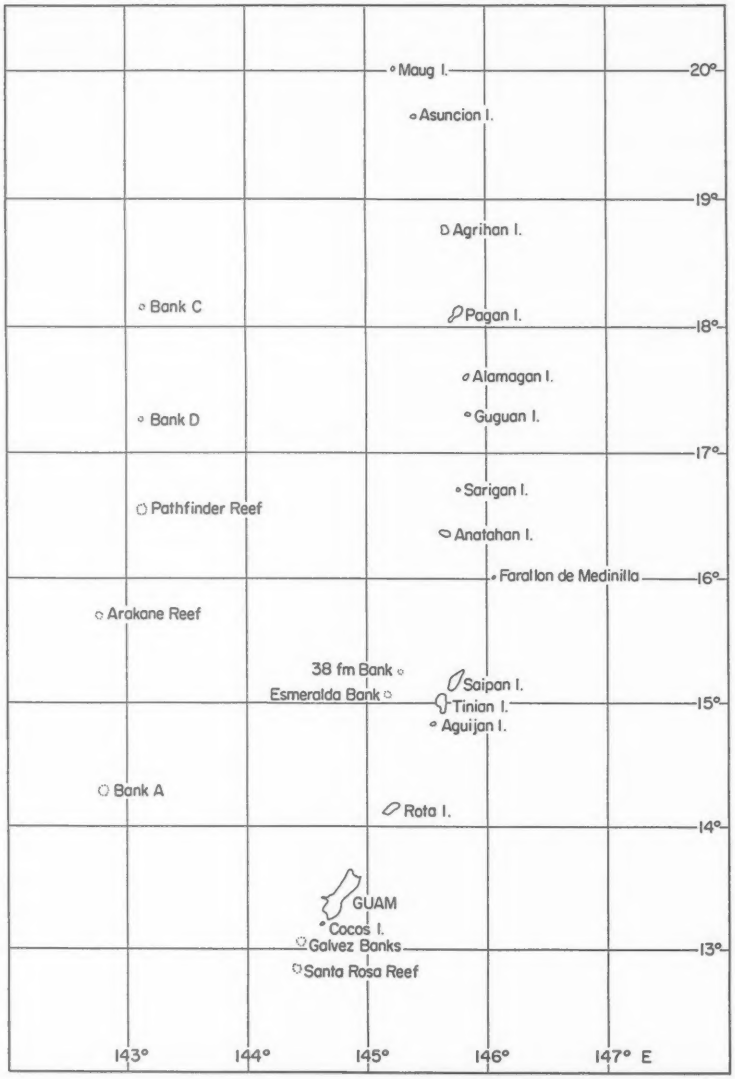

FIGURE 2.—The Mariana Archipelago with the 22 islands and banks sampled.

of three cruises. Two sites, Pagan Island and Esmeralda Bank, were sampled on each of the six cruises to establish a time series of length-frequency data.

The NOAA ship *Townsend Cromwell* was used as the fishing vessel for all the cruises. The fishing was conducted from four hydraulic gurdies equipped with 365 m of braided 90 kg Dacron[2] line. The terminal rig consisted of four hooks spaced about 1 m apart and of 2 kg weight.

At each island and bank, an attempt was made to perform a systematic fishing survey of the bottom fish community along the 200 m contour. Fishing was conducted while the vessel drifted and targeted the 125-275 m depth range. Fishing effort was measured in line-hours, defined as the product of the number of lines fished with the length of time, in hours, that they are fished.

Seven species—one jack, *Caranx lugubris*, and six snappers, *Pristipomoides zonatus*, *P. auricilla*, *P. filamentosus*, *P. flavipinnis*, *Etelis carbunculus*, and *E. coruscans*—accounted for about 92% of the catch (Polovina 1986b). Large length-frequency samples were collected for all seven species, primarily from the unfished islands and banks, and were used to jointly estimate M/K, the ratio of instantaneous natural mortality (M) to the growth parameter of the von Bertalanffy growth curve (K), and the asymptotic length (L_∞) by regressing a sequence of mean lengths on minimum lengths (Wetherall et al. in press). Otoliths were collected for all seven species and the growth coefficient K was estimated by fitting a von Bertalanffy growth curve to otolith data with L_∞ fixed at the value estimated from the length-frequency analysis (Ralston and Williams[3]). Once K and the ratio of M/K were estimated, an estimate of M was obtained from their product. The size of entry to the fishery was estimated as the integrated midpoint of the ascending limb of the size-frequency distribution (Gulland 1969). This size was then converted to an age of entry into the fishery (t_c) by application of the von Bertalanffy growth curve. The values of L_∞, K, M, t_m, and t_c for the seven species which are required by the yield analysis are given in Table 1. The exponent of the length-weight equation (b) for most of the species is not significantly different from 3.0, so to simplify the computation, it will be taken as 3.0 for all the species (Ralston in press).

An estimate of the catchability of the bottom fishes which was used to convert CPUE into standing stock was derived from an intensive fishing experiment conducted at Pathfinder Reef (Polovina 1986a). Thirteen days of intensive handline fishing with the *Townsend Cromwell* at Pathfinder Reef produced a substantial and significant decline in CPUE. Application of the Leslie model (Ricker 1975), which regresses CPUE against cumulative catch, produced estimates of catchability for three species—*Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus* (Polovina 1986a). While interesting differences in catchability among species were found, the estimate of the total unexploited biomass for the three species obtained from the species specific Leslie model was not significantly different from the total unexploited biomass computed from the Leslie model applied to the catch and CPUE data pooled over all three species. Catchability from the pooled Leslie model is estimated to be 0.0066 nmi/line-hour. This value was used as an estimate of total

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Ralston, S., and H. A. Williams. Age, growth, and mortality of deep slope lutjanid fishes from the Mariana Archipelago. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

TABLE 1.—Population parameters for the seven major species caught by handlining in the Marianas.

Species	Von Bertalanffy growth parameters		Instantaneous natural mortality (M)	Age of entry to the catch t_c (yr)	Age of maturity t_m (yr)
	L_∞ (cm)	K (1/yr)			
Caranx lugubris	75.1	0.430	0.53	1.3	1.8
Pristipomoides filamentosus	67.3	0.228	0.57	4.3	2.0
P. auricilla	42.6	0.335	0.81	3.6	2.4
P. flavipinnis	54.1	0.238	1.12	3.7	2.2
P. zonatus	47.0	0.245	0.63	4.65	3.25
Etelis coruscans	97.6	0.166	0.38	6.2	4.1
E. carbunculus	69.1	0.175	1.55	3.45	2.75

bottom fish catchability and was used to estimate standing stock from CPUE.

The systematic survey of relative abundance uses the fishing drift as the basic sampling unit. A drift is defined as the fishing which occurs during an uninterrupted drift by the vessel while fishing continuously in the 125-275 m depth range. The CPUE measured is the number of fish per line-hour and can be computed in two ways for each bank. Bank CPUE will be defined as the total number of fish caught at an island or bank divided by the total number of line-hours fished. Bank mean drift CPUE or simply mean drift CPUE will be defined as the mean of all the individual drift CPUE values for a bank, where the drift CPUE is computed as the number of fish caught within a drift divided by the drift line-hours. While the two measures of CPUE are highly correlated, they are not identical. In our analysis the mean drift CPUE was used as a measure of relative abundance because in a systematic survey the drifts within a bank can be thought of as replicates drawn from the total bank population allowing estimation of within bank variation in CPUE. For a bank, the total standing stock or number of exploitable bottom fishes (N) can be calculated from CPUE, the length (L) of the 200 m contour, and the catchability (q) expressed per nautical mile of 200 m contour as follows:

$$N = (\text{CPUE})\,(L/q).$$

The values of N, CPUE, and L for the banks sampled are given in Table 2.

The catch at any bank can be grouped into eight groups—the seven major species defined previously, plus a group called "others" for all other species. The fraction of the catch (by number) of the total bank catch as determined from fishing surveys, is given in Table 3. The mean weight of each species caught at each site is given in Table 4. For each bank, the unexploited recruited biomass (B_∞) for each of the eight groups is estimated by partitioning the total standing stock into a standing stock for each species group from Tables 2 and 3 and then converting the standing stock for each species group into biomass for each group based on the mean weights in Table 4. Estimates of B_∞ for the eight species groups at each bank are given in Table 5 and the total unexploited biomass is given in Table 6. The estimates of biomass per nautical mile of 200 m contour at Saipan, Tinian, Rota, and Guam are less than half the levels at most other banks. These four islands are the only islands in the Marianas with a substantial resident population. The local fishermen at these islands are known to exploit the bottom fish stocks locally so that estimates of biomass based on bank CPUE values are likely to underestimate unexploited levels. The mean of the biomass per nautical mile of 200 m contour for the two uninhabited islands and one bank in the southern islands is 600 kg. This value was used for unex-

TABLE 2.—Mean drift catch per unit effort (CPUE) and the estimated number of exploitable bottom fish recruited at each bank samples. SE indicates standard error.

Banks and islands	Mean drift CPUE (fish/ line-hour)	SE	Length of 200 m contour (nmi)	Total number of fish at each bank
Maug	5.03	1.02	10.4	7,580
Asuncion	2.16	0.49	11.1	3,480
Agrihan	4.20	0.31	18.3	11,140
Pagan	4.57	0.40	30.0	19,870
Alamagan	2.37	0.19	11.3	3,881
Guguan	3.01	0.30	9.3	4,060
Sarigan	2.82	0.37	8.5	3,470
Anatahan	2.31	0.23	17.2	5,760
Farallon de Medinilla	3.29	0.65	76.9	36,670
Saipan	1.72	0.34	52.6	13,110
38-Fathom	3.12	0.26	2.8	1,270
Tinian	1.96	0.29	28.9	8,210
Aguijan	3.84	0.98	15.9	8,850
Esmeralda	2.29	0.15	12.3	4,080
Rota	1.91	0.40	31.7	8,780
Guam	1.53	0.35	85.2	18,890
Galvez-Santa Rosa	2.95	0.31	52.5	22,450
Bank C	5.91	1.57	3.0	2,570
Bank D	5.85	0.51	3.0	2,540
Pathfinder	4.58	0.23	3.0	1,990
Arakane	3.36	0.24	2.9	1,410
Bank A	3.71	0.57	3.6	1,940

TABLE 3.—The fraction of the number of fish caught at each bank in the eight species groups.

Banks and islands	*Caranx lugubris*	*Pristipomoides filamentosus*	*P. auricilla*	*P. flavipinnis*	*P. zonatus*	*Etelis coruscans*	*E. carbunculus*	Others
Maug	0.016	0.000	0.347	0.016	0.425	0.000	0.102	0.094
Asuncion	0.036	0.036	0.089	0.000	0.589	0.018	0.036	0.196
Agrihan	0.016	0.041	0.103	0.064	0.602	0.016	0.110	0.048
Pagan	0.007	0.002	0.089	0.013	0.699	0.023	0.126	0.042
Alamagan	0.010	0.013	0.232	0.011	0.495	0.143	0.059	0.037
Guguan	0.020	0.004	0.182	0.004	0.613	0.047	0.083	0.047
Sarigan	0.016	0.010	0.141	0.010	0.646	0.042	0.057	0.078
Anatahan	0.015	0.035	0.119	0.148	0.540	0.040	0.045	0.059
38-Fathom	0.064	0.028	0.228	0.047	0.434	0.019	0.045	0.136
Esmeralda	0.017	0.051	0.040	0.366	0.397	0.029	0.026	0.074
Farallon de Medinilla	0.052	0.021	0.093	0.166	0.477	0.021	0.093	0.078
Saipan	0.013	0.138	0.087	0.338	0.225	0.000	0.075	0.125
Tinian	0.000	0.000	0.083	0.694	0.000	0.056	0.139	0.028
Aguijan	0.021	0.188	0.063	0.417	0.271	0.000	0.000	0.042
Rota	0.019	0.143	0.162	0.114	0.362	0.029	0.067	0.105
Guam	0.064	0.161	0.258	0.129	0.161	0.000	0.129	0.097
Galvez-Santa Rosa	0.085	0.017	0.364	0.051	0.322	0.009	0.059	0.093
Bank C	0.000	0.017	0.390	0.000	0.356	0.017	0.212	0.009
Bank D	0.015	0.010	0.091	0.005	0.480	0.045	0.349	0.005
Pathfinder	0.059	0.011	0.172	0.004	0.506	0.000	0.215	0.032
Arakane	0.116	0.057	0.188	0.003	0.412	0.000	0.169	0.055
Bank A	0.008	0.004	0.184	0.008	0.607	0.000	0.159	0.029

TABLE 4.—Mean weight (kg) of the fish caught by bank and species group.

Banks and islands	*Caranx lugubris*	*Pristipomoides filamentosus*	*P. auricilla*	*P. flavipinnis*	*P. zonatus*	*Etelis coruscans*	*E. carbunculus*	Others
Maug	3.784	1.930	0.815	1.585	0.977	6.113	0.893	2.559
Asuncion	3.784	1.930	0.848	1.265	1.344	6.113	0.670	4.595
Agrihan	3.784	1.930	0.784	1.235	1.169	6.113	0.741	7.787
Pagan	3.784	1.930	0.651	1.169	1.094	6.113	0.652	5.068
Alamagan	3.784	1.930	0.834	1.354	1.326	6.113	1.010	2.992
Guguan	3.784	1.930	0.773	1.780	1.216	6.113	0.815	2.400
Sarigan	3.784	1.930	0.642	1.025	1.204	6.113	0.811	5.279
Anatahan	3.784	1.930	0.556	1.169	0.874	6.113	0.586	2.631
38-Fathom	3.784	1.930	0.532	1.193	0.874	6.113	0.798	2.523
Esmeralda	3.784	1.930	0.567	1.014	0.782	6.113	0.702	8.409
Farallon de Medinilla	3.784	1.930	0.439	1.265	0.891	6.113	0.575	1.963
Saipan	3.784	1.930	0.577	0.992	0.837	6.113	0.773	1.353
Tinian	3.784	1.930	0.653	1.003	1.017	6.113	0.422	0.520
Aguijan	3.784	1.930	0.480	0.927	0.760	6.113	0.753	0.770
Rota	3.784	1.930	0.542	1.222	0.667	6.113	0.506	3.168
Guam	3.784	1.930	0.606	1.112	0.780	6.113	0.673	0.600
Galvez-Santa Rosa	3.784	1.930	0.522	1.206	0.979	6.113	0.801	2.085
Bank C	3.784	1.930	0.761	1.265	1.267	6.113	0.923	0.920
Bank D	3.784	1.930	0.961	1.710	1.169	6.113	0.983	1.070
Pathfinder	3.784	1.930	1.953	1.381	1.218	6.113	0.875	7.348
Arakane	3.784	1.930	0.860	1.350	0.949	6.113	0.791	2.338
Bank A	3.784	1.930	0.636	1.605	0.984	6.113	0.811	5.504

TABLE 5.—The unexploited recruited biomass by bank for each species groups in metric tons.

Banks and islands	*Caranx lugubris*	*Pristipomoides filamentosus*	*P. auricilla*	*P. flavipinnis*	*P. zonatus*	*Etelis coruscans*	*E. carbunculus*	Others
Maug	0.5	0	2.2	0.2	3.3	0	0.7	1.9
Asuncion	0.5	0.2	0.3	0	2.9	0.4	0.1	3.3
Agrihan	0.7	0.9	0.9	0.9	8.2	1.1	0.9	4.4
Pagan	0.6	0.1	1.2	0.3	15.9	2.9	1.7	4.4
Alamagan	0.1	0.1	0.8	0.1	2.7	3.5	0.2	0.5
Guguan	0.3	<0.1	0.6	<0.1	3.2	1.2	0.3	0.5
Sarigan	0.2	0.1	0.3	<0.1	2.8	0.9	0.2	1.5
Anatahan	0.3	0.4	0.4	1.0	2.8	1.5	0.2	0.9
38-Fathom	0.3	0.1	0.2	0.1	0.5	0.2	<0.1	0.5
Esmeralda	0.3	0.4	0.1	1.6	1.3	0.7	0.1	2.7
Farallon de Medinilla	7.5	1.5	1.6	8.0	16.3	4.9	2.1	5.8
Saipan	0.6	3.6	0.7	4.6	2.6	0	0.8	2.3
Tinian	0	0	0.5	6.0	0	2.9	0.3	0.1
Aguijan	0.7	3.3	0.3	3.6	1.9	0	0	0.3
Rota	0.7	2.6	0.8	1.3	2.2	1.6	0.5	3.1
Guam	4.8	6.1	3.1	2.8	2.5	0	1.7	1.1
Galvez-Santa Rosa	7.5	0.8	4.5	1.4	7.4	1.2	1.1	4.6
Bank C	0	0.1	0.8	0	1.2	0.3	0.5	<0.1
Bank D	0.2	0.1	0.2	<0.1	1.5	0.7	0.9	<0.1
Pathfinder	0.5	<0.1	0.4	<0.1	0.3	0	0.4	0.5
Arakane	0.6	0.2	0.2	<0.1	0.6	0	0.2	0.2
Bank A	0.1	<0.1	0.2	<0.1	1.2	0	0.3	0.3
Total	32.5	32.0	24.5	43.1	85.4	26.2	15.9	42.8

TABLE 6.—The total unexploited recruited biomass (B_∞) in metric tons (t) and the total unexploited recruited biomass per nautical mile (nmi) of 200-m contour in kilograms (kg) by bank.

Banks and islands	Total unexploited recruited biomass (t)		Biomass per nmi of 200 m contour (kg)
Northern banks and islands			
Maug	8.8		850.3
Asuncion	7.7		689.7
Agrihan	18.1		991.1
Pagan	27.0		900.7
Alamagan	8.0		706.8
Guguan	6.1		659.7
Sarigan	6.1		714.0
Anatahan	7.6		440.6
38-Fathom	1.8		637.1
Esmeralda	7.2		584.1
	Total 98.4	Mean	717.4
Southern banks and islands			
Farallon de Medinilla	47.7		620.2
Saipan	15.3		290.9
Tinian	10.0		346.0
Aguijan	10.1		637.0
Rota	12.4		391.2
Guam	22.2		260.6
Galvez-Santa Rosa	28.5		542.4
	Total 146.2	Mean	441.2
Western seamounts			
Bank C	2.9		973.0
Bank D	3.6		1,207.0
Pathfinder	3.1		1,024.0
Arakane	2.0		695.9
Bank A	2.1		594.7
	Total 13.7	Mean	898.9

ploited biomass per nautical mile of 200 m contour in the subsequent yield estimation, in place of the values computed from the bank CPUE values for the inhabited southern islands (Saipan, Tinian, Rota, and Guam).

For each species group with values of K, M, t_c, and F, the ratio of fishery yield to unexploited recruited biomass (Y/B_∞) can be computed from the Beverton and Holt yield equations (Beddington and Cooke 1983). The product of Y/B_∞ with the species group unexploited recruited biomass estimates (Table 5) results in estimates of equilibrium yield for the seven species for which estimates of K and M are available. For the eighth group, which consists of all other species, the ratio of yield to B_∞ is taken as the ratio of total yield for the seven species divided by their total B_∞. For a fixed F, the sum of the equilibrium yield of the eight species groups at a bank is the bank equilibrium yield, and the sum of the equilibrium yields for a species group over all the banks is the species group equilibrium yield.

The equilibrium yield for the multispecies bottom fish complex fished with handline gear in the 125-275 m depth range for the 22 islands and banks of the Mariana Archipelago increases rapidly as a function of F to a level of about 90 t and beyond that exhibits a gradual increase with increased fishing mortality (Table 7). The MSY estimation approach estimates MSY as the yield from the constant recruitment yield curve corresponding to that level of mortality where a marginal increase in one unit of mortality increases the catch by 0.1 of the amount caught by the first unit of F. The value of $F_{0.1}$ for the bottom fish resource in the Marianas is estimated to be $F = 1.0$ and the corresponding annual equilibrium yield is 82 t (Table 7).

The equilibrium yield value of 82 t, which corresponds to a fishing mortality of 1.0, is based on the current estimated age of entry to the fishery and not necessarily the age of entry which maximizes the Y/R. For a fishery mortality of 1.0, the estimated age of entry which maximizes Y/R is computed from the Beverton and Holt equation and compared with the current age of entry for each species (Table 8). With the exception of the jack, *Caranx lugubris*, the age of entry which maximized Y/R is less than the current age of entry (Table 8). Based on the age of entry which maximized the Y/R, new levels of sustainable yield for each species group as a function of F can be computed as the product of the yield for the current age of entry with the ratio of Y/R maximized over age of entry to the Y/R for the current age of entry. The values of $F_{0.1}$ and $Y_{0.1}$ for the ages of entry which maximize the Y/R are 1.0 and 109 t, respectively (Table 9). An approximate confidence interval (C.I.) for this yield estimate can be obtained from a Taylor series expansion which incorporates the variance estimate for catchability (Polovina 1986a) and a sampling variance of the bank CPUE values (Table 2). The standard error of the yield estimate is 14 t, and thus a 95% C.I. for the yield at $F_{0.1}$ for the archipelago is 81-137 t annually.

The estimation of MSY based on the relative spawning stock approach requires estimates of the age of sexual maturity (t_m). A relationship expressing the length at sexual maturity (L_m) as a fraction of the length of the upper one percentile (L_{max}) for tropical bottom fishes is as follows (Anonymous 1977, from Brouard and Grandperrin 1984):

$$L_m = 0.576\, L_{max}.$$

TABLE 7.—Total annual sustainable handline yield in metric tons (t) for a range of fishing mortalities.

Fishing mortality (F)	Total yield (t)
0.1	23
0.5	64
[1]1.0	[1]82
1.5	89
2.0	92
2.5	94

[1]$F_{0.1}$ and $Y_{0.1}$ as defined by Gulland (1983).

TABLE 8.—Current age at entry and age at entry which maximizes the yield per recruit (Y/R) at $F = 1.0$.

Species	Current age at entry t_c (yr)	Age at entry which maximizes Y/R (yr)
Caranx lugubris	1.3	1.75
Pristipomoides filamentosus	4.3	2.75
P. auricilla	3.6	2.25
P. flavipinnis	3.7	2.00
P. zonatus	4.65	3.00
Etelis coruscans	6.2	4.50
E. carbunculus	3.45	2.50

TABLE 9.—Annual sustainable handline yield in metric tons (t) for the age at entry which maximizes the yield per recruit for each species.

Fishing mortality (F)	Total yield (t)
0.1	35
0.5	91
[1]1.0	[1]109
1.5	114
2.0	116
2.5	116

[1]$F_{0.1}$ and $Y_{0.1}$ as defined by Gulland (1983).

The t_m can then be computed from L_m with the von Bertalanffy growth equation. The t_m for the seven species, which is assumed to be the same for both sexes of a species, is given in Table 1, and the ratio of spawning stock biomass under exploitation to the unexploited spawning stock biomass is presented for three levels of F (Table 10). As expected, the ratio decreases as F increases. However, without the spawner-recruit relationship, it is difficult to determine the extent that the spawning stock biomass can be reduced before recruitment is substantially affected. It has been suggested that as a lower bound, the spawning stock biomass should not be reduced below 20% of its unexploited level before there is a deleterious reduction in recruitment (Beddington and Cooke 1983). The level of $F = 1.0$ is the largest level of F which insures that the relative spawning stock biomass for all the species does not fall below 20% and hence the spawning stock approach also estimates the MSY for the bottom fish in the Marianas at 109 t/year.

TABLE 10.—The ratio of spawning stock biomass to unexploited spawning stock biomass for three levels of fishing mortality (F) at the age of entry which maximizes the yield per recruit.

Species	$F = 0.5$	$F = 1.0$	$F = 2.0$
Caranx lugubris	0.44	0.26	0.12
Pristipomoides filamentosus	0.46	0.33	0.25
P. auricilla	0.45	0.29	0.19
P. flavipinnis	0.45	0.26	0.12
P. zonatus	0.39	0.24	0.14
Etelis coruscans	0.31	0.20	0.13
E. carbunculus	0.58	0.42	0.30

DISCUSSION

The assessment proposed here is a multispecies approach which is most suitable for resources where prey-predator interactions are negligible. Two assumptions initially required to implement this program, i.e., constant recruitment and that the resource be essentially unexploited, can in some instances be relaxed. Simulation results suggest that if recruitment is seasonal and a pooled length frequency is constructed from individual length-frequency samples collected over the year, the length-frequency based method used here to estimate mortality produces an essentially unbiased estimate (Ralston[4]). Furthermore, the assumption that stocks be unexploited can be relaxed if an estimate of the average of F for the archipelago can be obtained. Then M can be estimated by the difference between F and total mortality, and instead of estimating unexploited recruited biomass from the CPUE survey, the biomass under F will be estimated, and yields calculated as the product of exploited biomass with the ratio of yield/biomass resulting from F computed from the Beverton and Holt yield equation.

The estimate of maximum equilibrium yield from the Beverton and Holt (1957) equation for the deep slope snappers and groupers from 22 banks in the Mariana Archipelago is 109 t annually with a fishing mortality of 1.0. About 70% of this yield would be expected to come from the southern islands of the chain, including Guam and Saipan. Another 27% would come from the northern islands and only 3% from the seamounts (Table 11).

The mean of the annual sustainable yield levels per nautical mile of 200 m contour for the northern banks, southern banks, and western seamounts are 212.9, 228.5, and 264.4 kg, respectively, with a ratio of total yield for the archipelago to the total length of the 200 m contour of 222.4 kg/nmi (95%) C.I. of 165.3-279.6) (Table 11). Detailed bathymetry data to establish a correspondence between contour length and area are available from Guguan Island in the northern Marianas, and it is estimated that 1 nmi of 200 m isobath corresponds to 0.23 nmi^2 of habitat in the 125-275 m depth range (Polovina and Roush[5]). Based on this correspondence the unit MSY of 222.4 kg/nmi of 200 m contour for the Marianas is equivalent to about 1.0 t/nmi^2 or 0.3 t/km^2.

These values suggest that the Marianas may be slightly less productive for bottom fishes than the Hawaiian Archipelago where a lower bound estimate for MSY of 272 kg/nmi of 200 m contour was obtained from a stock production model applied to commercial catch and effort data that did not include the recreational fishing component of snappers and groupers. Also, an estimate of 286 kg/nmi of 200 m contour was derived from an ecosystem model applied to an island system in the Northwestern Hawaiian Islands (Ralston and Polovina 1982; Polovina 1984).

The species composition of the catch should depend to some extent on levels of F and t_c. As F increases and t_c decreases, the contribution of

[4]Ralston, S. The effect of pooling length-frequency distributions on mortality estimation in seasonally breeding fish populations: A Monte Carlo simulation. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

[5]Polovina, J. J., and R. C. Roush. 1982. Chartlets of selected fishing banks and pinnacles in the Mariana Archipelago. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. H-82-19, 7 p.

TABLE 11.—Annual sustainable yield in metric tons (t) and yield in kilograms (kg) per nautical mile (nmi) of 200 m contour for the age at entry which maximizes the yield per recruit at a level of fishery mortality of $F = 1.0$.

Banks and islands		Total yield (t/yr)		Yield (kg per nmi of 200 m contour/yr
Northern banks and islands				
Maug		2.7		262
Asuncion		2.1		188
Agrihan		5.6		304
Pagan		7.7		255
Alamagan		2.0		178
Guguan		1.7		179
Sarigan		1.6		194
Anatahan		2.5		144
38-Fathom		0.5		187
Esmeralda		2.9		237
	Total	29.3	Mean	213
Southern banks and islands				
Farallon de Medinilla		16.7		217
Saipan		13.4		254
Tinian		8.8		304
Aguijan		4.2		267
Rota		6.1		192
Guam		17.2		202
Galvez-Santa Rosa		8.6		164
	Total	76.0	Mean	229
Western seamounts				
Bank C		0.9		288
Bank D		1.1		351
Pathfinder		0.9		304
Arakane		0.6		200
Bank A		0.6		180
	Total	4.1	Mean	264
Total yield from all banks: 109 t/yr.				
Total yield/length of 200 m contour = 222.3 kg/nmi.				

those species to the catch with the high M/K values, particularly *P. flavipinnis* and *E. carbunculus* tends to increase (Table 12). A form of succession is, therefore, predicted as exploitation proceeds.

There are two approximations which have been used to determine MSY which express it as a fraction of the unexploited biomass. Gulland's formula estimates MSY as $0.5\,MB$, where M is the instantaneous rate of natural mortality and B is the unexploited biomass. An approach proposed by Pauly estimates MSY as $B\,2.3w^{-0.23}$, where w is the mean of the weight (in grams) at sexual maturity and the asymptotic weight (Gulland 1983; Pauly 1983). A comparison of these two estimators with the values obtained here shows that for four out of seven species the Y/B values estimated with the Beverton and Holt equation lie between the values obtained from the Pauly and Gulland approximations.

TABLE 12.—The percentage of annual sustainable yield by species groups for two ages at entry with two levels of fishing mortality.

	Percentage of total catch by weight			
	Current age of entry		Age at entry which maximizes yield per recruit	
Species groups	$F = 0.10$	$F = 1.50$	$F = 0.10$	$F = 1.0$
Caranx lugubris	10.0	5.5	7.3	8.3
Pristipomoides filamentosus	10.3	8.5	9.4	8.2
P. auricilla	8.5	9.4	7.4	7.3
P. flavipinnis	15.6	21.7	24.3	28.7
P. zonatus	28.1	26.7	26.1	23.1
Etelis coruscans	7.6	5.1	7.1	5.0
E. carbunculus	5.9	9.2	4.6	5.9
Others	14.0	13.8	13.8	13.5

For the other three species, the Y/B values fall slightly below the Pauly and Gulland approximations for two species and substantially above for the third species. The mean Y/B values obtained by the Pauly and Gulland approximations are, moreover, in substantial agreement with the mean value of Y/B obtained with the approach proposed here (Table 13).

TABLE 13.—Annual maximum sustainable yield as a fraction of unexploited recruited biomass (Y/B_∞) at $F = 1.0$ together with 0.5 M and 2.3 $w^{-0.26}$.

Species groups	Y/B_∞	0.5 M	2.3 $w^{-0.26}$
Caranx lugubris	0.261	0.335	0.252
Pristipomoides filamentosus	0.262	0.270	0.296
P. auricilla	0.306	0.325	0.403
P. flavipinnis	0.680	0.475	0.348
P. zonatus	0.280	0.270	0.363
Etelis coruscans	0.201	0.175	0.226
E. carbunculus	0.375	0.515	0.289
Mean	0.338	0.338	0.311

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LITERATURE CITED

ANONYMOUS.
1977. Inventaire critique des données utilisées pour l'étude de la reproduction. *In* Rapport du groupe de travail sur la reproduction des espèces exploitées du Golfe de Guinée, p. 8-20. ORSTOM-ISRA, Dakar.

BANNEROT, S. P., AND C. B. AUSTIN.
1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. 112:608-617.

BEDDINGTON, J. R., AND J. G. COOKE.
1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.

BEVERTON, R. J. H., AND S. J. HOLT.
1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-v. Réun. Cons. int. Explor. Mer 140:67-83.
1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, vol. 19, Mar. Fish., G. B. Minist. Agric. Fish. Food, 533 p.
1966. Manual of methods for fish stock assessment. Part II. Tables of yield functions. FAO Fish. Tech. Pap. 38 (Rev. 1), 67 p.

BROUARD, F., AND R. GRANDPERRIN.
1984. Les poissons profonds de la pente recificale externe à Vanuatu. Mission ORSTOM, Vanuatu, Notes et Documents D'Océanographie 11, 131 p.

CSIRKE, J., AND J. F. CADDY.
1983. Production modeling using mortality estimates. Can. J. Fish. Aquat. Sci. 40:43-51.

GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Fish. Ser. 3, 154 p.
1983. Fish stock assessment. A manual of basic methods. John Wiley & Sons, 223 p.
1984. Advice on target fishery rates. ICLARM Fishbyte 2(1):8-11.

MUNRO, J. L.
1983. A cost-effective data acquisition system for assessment and management of typical multispecies, multi-gear fisheries. ICLARM Fishbyte 1(1):7-12.

PAULY, D.
1983. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap. (234), 52 p.

PAULY, D., AND G. I. MURPHY (editors).
1982. Theory and management of tropical fisheries. ICLARM Conf. Proc 9, 360 p. ICLARM, Manila, Philippines, and Division of Fisheries Research, CSIRO, Cronulla, Australia.

POLOVINA, J. J.
1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1-11.
1986a. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. Fish. Bull., U.S. 84:423-428.
1986b. Variation in catch rates and species composition in handline catches of deepwater snappers and groupers in the Mariana archipelago. Proc. 5th Int. Coral Reef Congr. 1985, Tahiti.

RALSTON, S.
1986. An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago Fish. Bull., U.S. 84:927-934.
In press. Length-weight regressions and condition indices of lutjanids and other deep slope fishes from the Mariana Archipelago. Micronesica.

RALSTON, S., AND J. J. POLOVINA.
1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull., U.S. 80:435-448.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

SAILA, S. B., AND P. M. ROEDEL (editors).
1979. Stock assessment for tropical small-scale fisheries. Proceedings of an International Workshop Held September 19-21, 1979, at the University of Rhode Island, Kingston, RI, 198 p.

WETHERALL, J. A., J. J. POLOVINA, AND S. RALSTON.
In press. Estimating growth and mortality in steady state fish stocks from length-frequency data. *In* D. Pauly and G. R. Morgan (editors), Length-based methods in fishery research. The ICLARM/KISR Conference on the Theory and Application of Length-Based Methods for Stock Assessments, Sicily, Italy, February 1985. Vol. 1.

GROWTH, BEHAVIOR, AND SEXUAL MATURATION OF THE MARKET SQUID, *LOLIGO OPALESCENS*, CULTURED THROUGH THE LIFE CYCLE

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ABSTRACT

Loligo opalescens, a commercially important species of the eastern Pacific, is the first pelagic cephalopod to be cultured through the entire life cycle. Squid were cultured twice to viable second generation progeny in closed seawater systems using artificial and natural seawater. The reasons for success compared with previous attempts were 1) increased depth in the culture tank, 2) improvements in water conditioning methods, and 3) an increase in availability, density, and species diversity of food organisms. The diet consisted of live zooplankton (predominantly copepods), mysid and palaemonid shrimp, and estuarine fishes. Mean daily group feeding rates of subadults and adults were 14.9% and 18.0% of body weight. Growth was fast, increasing exponentially the first 2 months of the life cycle (8.35% increase in body weight per day) then slowing to a logarithmic rate thereafter (5.6-1.6% increase per day). Growth rings in statoliths corresponded to one per day for the first 65 days. Maximum life span was 235 and 248 days in the two experiments, with a maximum size of 116 mm dorsal mantle length. Viable eggs were produced within 172 and 196 days, respectively. Eggs developed in 30 days at 15°C. Survival through the life cycle was low, with the highest mortality occurring in the first few weeks when squid made the transition from feeding on yolk to active predation on fast-moving plankton. Fin or skin damage and senescence after reproduction accounted for late mortality. The laboratory life cycle of less than a year is compatible with existing field data that propose either a 1- or 2-year life cycle, depending upon the season of hatching.

Since 1975 we have been studying loliginid squid to develop methods of providing a consistent supply for neuroscience research. These studies include aspects of fishery biology (Rathjen et al. 1979; Hixon 1980a, b, 1983; Hixon et al. 1980), capture and maintenance methods (Hanlon et al. 1978, 1983; Hulet et al. 1979; Hanlon and Hixon 1983), behavior (Hanlon 1978, 1982), and mass-culture methods (Hanlon et al. 1979; Yang et al. 1980a, b, 1983a, b). Much of the baseline information acquired through these controlled culture experiments will also be important to the fisheries biology of commercially exploited loliginid squids (cf., Roper et al. 1983).

About 20 major attempts have been made to culture loliginid squids through the life cycle, but none have been successful (see review in Yang et al. 1980b), even though wild-caught mature females of *Loligo* and *Doryteuthis* spawn readily in captivity (Hamabe 1960; Fields 1965; Takeuchi 1969, 1976; Hurley 1977; Arnold et al. 1974; Hanlon et al. 1983). Fields (1965) attempted unsuccessfully to culture *Loligo opalescens* as early as 1947. Hurley (1976) reared *L. opalescens* for 100 d to a mantle length (ML) of 13 mm. Hanlon et al. (1979) reared this species to 17 mm ML in 79 d and, based upon that work, reared *L. opalescens* from hatching to subadults (Yang et al. 1980b, 1983a). We have now improved previous culture methods by increasing the rearing population density and by improving the space requirements for young and adult squid. With a more consistent supply of foods and improvement of water management, we have now successfully cultured this squid twice from egg to second generation, thus closing the life cycle.

MATERIALS AND METHODS

Two culture experiments are reported herein: L.O. 1981 (full life cycle partly published in Japanese by Yang et al., 1983b); and L.O. 1982 (full life cycle). A third experiment, L.O. 1980, was published by Yang et al. (1980b, 1983a) and is referenced for comparison in the Discussion and figures.

For L.O. 1981, freshly laid eggs were obtained from wild-caught squid kept in holding tanks at Sea Life Supply (Sand City, CA 93955). Eggs were collected from spawning grounds in Monterey Bay, CA for experiment L.O. 1982. Eggs were air-shipped

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to Galveston (Yang et al., 1980b; 1983a, b). Only early stage eggs were shipped and cultured (never beyond stage 19, Arnold 1965). The eggs were acclimated gradually to the temperature and salinity of the culture tank water; incubation temperature was maintained around 15°C while salinity ranged between 34 and 36‰. Bundles of a few capsules each were suspended from a rack at the water surface to ensure oxygenation and uniform development of eggs. Styrofoam panels covered the rearing tank and the illumination level was kept below 1 lux to prevent the growth of benthic diatoms on egg capsules.

A circular tank (CT) system consisting of two circular tanks (each 1,300 L) was used for incubation and early rearing of hatchlings and juvenile squid. Water circulation was modified in L.O. 1982 when compared with earlier culture experiments (Yang et al. 1980b: fig. 1, 1983a: fig 1). Prior to L.O. 1982, a laboratory-constructed particle/carbon filter was used with circulation first passing through an ultraviolet (UV) sterilizer. L.O. 1982 used modular type particle and carbon filters, with the UV sterilizer in the last position in the water conditioning process. The raceway (RW) system (RW culture tank volume—10,970 L in L.O. 1981, and 13,180 L in L.O. 1982) was used for final grow-out after transferring the squid from the CT culture tanks. The transfer was necessary to give the squid greater horizontal swimming space. The initial RW system in experiment L.O. 1981 had been modified from previous experiments (Yang et al. 1980b, 1983a) to improve water quality by 1) adding a rectangular, 960 L capacity water conditioning tank (0.46 × 1.22 × 1.83 m, water depth 0.43 m) with water circulation of 54 L/minute, 2) adding another cooling unit, 3) adding three protein skimmers, 4) adding three UV light sterilizers (each 30 W, total 90 W), 5) modifying the water uptake system in the RW with a float near the center to remove near-surface water without sucking up squid or food organisms and to increase the lateral swimming space for the squid, 6) painting an irregular mottled pattern on the sides of the RW to make the walls more visible to the squid, and 7) most importantly, by increasing RW water depth gradually from 24 cm initially to 40 cm (average depth 38.8 cm) to provide swimming space for the squid and to increase the average culture water volume in the RW from 5,990 to 8,610 L.

A further improved RW system (Fig. 1) was used in experiment L.O. 1982. It consisted of two biological filter tanks (A, C) with oyster shell subgravel filters and airlifts for water circulation, a tank for growing macroalgae (B), the RW where the squid were cultured (D), and a separate tank where protein skimmers were operated continuously (E). The surface water was taken from the RW through pipes suspended in a screened floating core. Water within the system was recirculated by three routes. First, water was pumped to filter tank A that contained approximately 0.15 m^3 of oyster shell over a false bottom. Water passed through the filter bed, then flowed through a constant-level siphon to tank B where algae were illuminated by two 400-W metal halide lamps. Water flowed by gravity into the second filter tank C that contained 0.18 m^3 of oyster shell substrate and two 1-hp cooling units, and finally returned by gravity to the RW proper. Second, water was pumped through two sets of six modular filters: four modules containing pleated 20 μm fiber particle filters and two containing activated carbon. From the modular filters, water either flowed directly into the RW or through a 60 W UV sterilizer before returning to the RW. Third, water was pumped at 36 L/minute to a tank that contained five protein skimmers and then flowed back into the RW. The outflow of the three recirculating routes created a clockwise water flow in the RW proper. This motion accumulated dead squid and food organisms in one place on the bottom. The bottom was painted solid black with nontoxic Thixochlor[2] paint and the sides were painted with an irregular mottled pattern. Three 11 × 28 cm windows were mounted in one side of the RW for observing the squid's feeding and behavior. The tanks were insulated with polystyrene sheeting and 2.3 cm thick polystyrene covers.

To ensure activation of the biological filter for both CT and RW systems, filter beds were inoculated 2 to 3 wk beforehand with nitrifying bacteria on oyster shell from other systems. Fish and shrimp were placed in the water conditioning tank to build up the bacterial population. Thus the filter beds were established by organic conditioning methods (Moe 1982) instead of by directly adding ammonia source chemicals.

A set of black silk nets was used to transfer squid from the CT system into the RW system. A triangular lift net was laid on the bottom of the tank while two rectangular net curtains were slowly drawn from the left and right sides of the tank to concentrate the small squid above the lift net. The lift net was gradually raised, a wash tub placed underneath, and both were moved to the RW tank where the squid were gently released into the tank.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

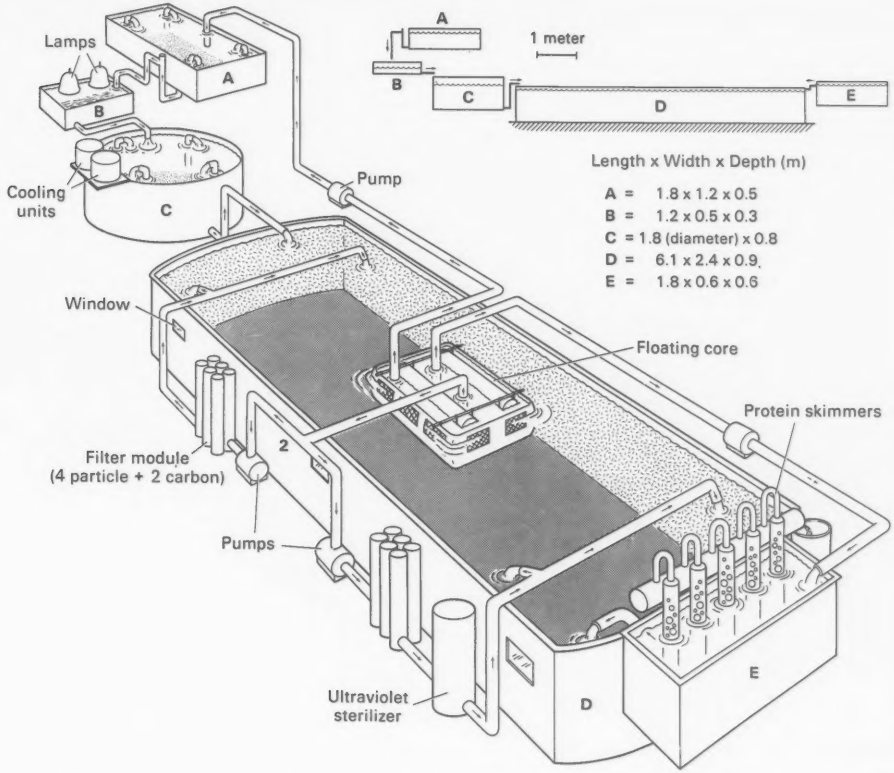


FIGURE 1.—Raceway (RW) system (L.O. 1982) with recirculating culture seawater (17,000 L total) for grow-out of juvenile and adult squid.

In L.O. 1981, 129 squid were not transferred from the CT tank and they continued to grow in the CT, thereby allowing comparisons of temperature tolerance and survival in small versus large culture systems.

Natural seawater and artificial sea salts (Instant Ocean) dissolved in deionized water were used in CT systems for L.O. 1982 and L.O. 1981, respectively, and artificial seawater was used exclusively in the RW system in both experiments. Salinity was maintained between 34 and 37‰. Trace elements were supplemented regularly with Wimex Trace Elements. Temperature was maintained at 15°C unless otherwise noted. The pH was maintained between 7.8 and 8.2, and low pH was corrected by the gradual addition of sodium bicarbonate.

Temperature and salinity were measured daily, pH every other day, and metabolic waste products (ammonia, nitrite, and nitrate) were measured weekly. Ammonia-nitrogen levels were determined by the Solorzano method (Strickland and Parsons 1972), and nitrite-nitrogen was determined by the Shinn method (applied to seawater by Bendschneider and Robinson in Strickland and Parsons 1972). Nitrate-nitrogen levels were determined using a prepacked Hach reagent kit.

Various live food organisms were fed to the squid several times daily throughout the experiments. Live planktonic organisms such as zooplankton (mainly copepods) and small mysidacean shrimp (*Mysidopsis almyra*) were the primary foods during the first 60 d in the CT system. Brine shrimp, *Artemia salina*; larval red drum, *Sciaenops ocellatus*; and mysis stage penaeid shrimp were fed as supplemental foods. Food organisms were added to the CT system four or five times daily. Thereafter

in the RW system, adult mysids; palaemonid shrimp, *Palaemonetes pugio*; and a variety of marine or estuarine fishes were fed to the squid at least twice daily.

Zooplankton were washed carefully in clean seawater. Mysids and palaemonid shrimp were treated overnight with quinacrine, while erythromycin and/or tetracycline were used to treat fish (Yang et al. 1980b, 1983a, b). Before feeding, all foods were counted or weighed and slowly acclimated to the temperature and salinity of the cultured water.

Dead squid and dead food organisms from previous feedings were removed by siphoning once or twice daily from the CT or RW systems. Daily food consumption in the RW was derived by subtracting the weight of uneaten food remains siphoned each day from the weight of food organisms added daily to each culture system. Daily feeding rate (wet weight) is expressed as the percentage of food consumed by the total estimated biomass of the squid. Daily biomass of squid was estimated by multiplying the number of live squid on a given day by the average weight of an individual squid on that day. Daily squid weight estimates were projected from linear regression of the weights of freshly dead squid against time. All measurements and wet weights (WW) were usually made with freshly dead squid although live squid were occasionally used. Badly damaged or partially cannibalized squid were not measured or weighed for this analysis. The initial squid population was derived from the number of dead or sacrificed specimens removed from the culture systems.

Overhead fluorescent lights provided illumination. In the CT systems for both experiments there was constant light that measured 11 to 15 lux in the middle of the water column. In the RW systems there was also constant light although light only filtered in through plastic-covered holes in the polystyrene tops. In L.O. 1981 it measured 17 lux in the center of the RW and 0.5 to 0.7 lux at each end. In L.O. 1982 it measured 4 to 7 lux near the ends under the opaque top and 11 lux near the center where light passed through the clear plastic.

Statoliths from hatchlings of known age in L.O. 1982 were dissected from the squid and decalcified in a 1:1 mixture of 4% EDTA in distilled water and 0.2 H sodium cacodylate buffer (pH 7.4). Decalcification facilitated the counting of rings in statoliths from squid age 65 d or younger, but older statoliths were distorted by the process. The rings were counted from photographs taken with a Leitz Combiphot II and Kodak copy film #4125.

RESULTS

Water Quality

There were no obvious differences in growth or survival between squid cultured in artificial seawater (L.O. 1981) and filtered natural seawater (L.O. 1982). Water quality in the CT systems was maintained in very good condition due to the short culture period, while water quality in the RW system was more difficult to maintain because of the long grow-out period and the greater biomass of squid and food organisms. In L.O. 1981 (Fig. 2) from days 180 to 190 the estimated total biomass reached the maximum peak of 1,706 g (cf., Fig. 7), which is equivalent to 155 g/m^3 of rearing water volume. After the 160th day, food organism biomass increased to between 300 and 400 g/day. As a result, the amount of nitrate-nitrogen gradually accumulated to over 23.0 mg/L during the period from day 180 to day 193 (Fig. 2). On day 164, 1,900 L (17% of total volume) of fresh Instant Ocean was replaced in this system. However, the nitrate-nitrogen level did not drop in proportion to the percent water change. Concurrently, pH dropped to 7.75 by day 169 and dissolved sodium bicarbonate (Atz 1964; Bower et al. 1981) was introduced to the system to adjust the pH above 7.9. The sodium bicarbonate solution required very strong aeration to be effective when it was put into the culture water. A similar trend of slightly increased nitrate-nitrogen and decreased pH occurred (about day 200) in L.O. 1982 (Fig. 2). This was corrected in the same manner.

The vegetative macroalgae, *Gracilaria tikvahiae*, was cultured in the water conditioning tank of the RW system in L.O. 1982 to remove ammonia and prevent the accumulation of nitrate-nitrogen, but its effectiveness was not clear.

Incubation and Hatching of Eggs

Average hatchling size in both experiments was 2.7 mm ML (range 2.3-2.8 mm ML) with a hatching success of over 90%. In L.O. 1981, hatching began on 14 October and lasted until 17 October. Embryonic development required 27 to 30 d at 15°C. The hatching period lasted 4 d, compared with L.O. 1982 that took 5 to 6 d. The period of embryonic development in L.O. 1982 was not precisely known because the eggs were collected in nature. Development of eggs within the same egg cluster was different depending upon the capsule position within the cluster. Moreover, hatching time within the same capsule

differed, since distal embryos usually hatched first. Since we used early stage eggs removed from their habitat in California, no polychaete worms (*Capitella ovincola*) were observed in the egg capsules (cf., McGowan 1954), although we had observed worms in other late stage California egg capsules.

During embryonic development, granules or crystals appeared in the perivitelline fluid of some eggs, but no significance to survival or development could be associated with this condition. The outer tunics of the egg capsules incubated in Instant Ocean were more elastic until the later stages (around stage 27) than those incubated in natural seawater. More bacteria and other benthic organisms grow on the capsules incubated in natural seawater. These differences did not influence development or hatching success. Embryos near hatching (stage 29) generally moved little or were nearly static, but in most individuals the external yolk sac was already broken off within the egg. External yolk sacs were observed on a few hatchlings. In L.O. 1981, bright illumination stimulated hatching in very late stage eggs and therefore light levels were increased during later stages of egg development in L.O. 1982.

Foods and Feeding

The species and size of food organisms were similar in the two experiments. The general progression of food types began with zooplankton, then mysidean shrimps, then palaemonid shrimp larvae and adults, and finally fishes (Fig. 3). The use of brine shrimp has been curtailed since they were found to be unattractive to the hatchlings.

The size range of food organisms fed in the first 30 d is large, especially when compared with the size of 1-d-old hatchlings (2.3-2.8 mm ML, Fig. 4). However, as shown in Figure 4, the hatchlings have only small fins and are not strong swimmers; therefore, feeding on active prey at this stage is not excellent. A summary of the types and quantities of food offered in the experiments (L.O. 1981 is used as an example) is given in Figure 5. Large amounts of food were available to the squid; this was important during the first weeks when hatchlings could only capture food organisms drifting very close to them. The relationship of hatchling to food organism density during the first 59-d period in each experiment is summarized in Table 1. Unfortunately there was no clear relationship between densities and survival. For example, in L.O. 1982, there were twice as many food organisms per squid as in L.O. 1981, but survival (cf., Fig. 13) was not better. Figure 5 shows more specifically the number of food organisms fed daily in L.O. 1981.

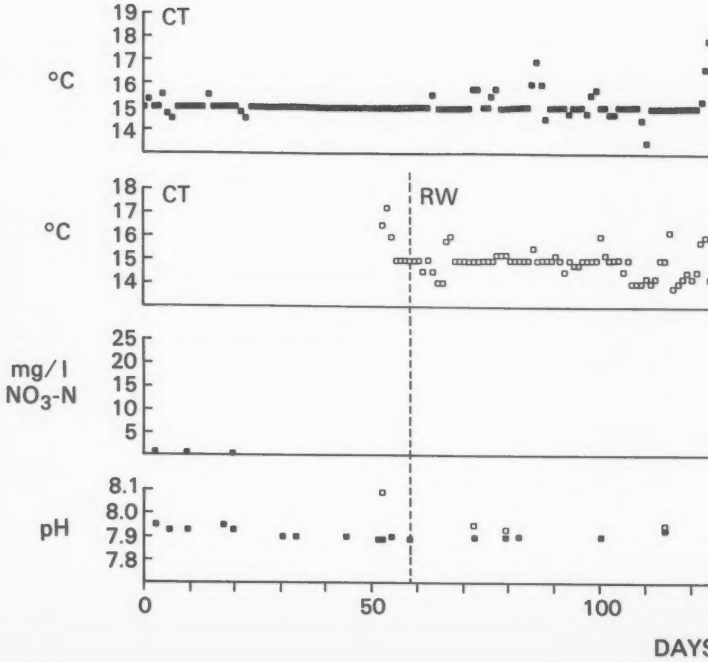
The early rearing period in L.O. 1981 and 1982 coincided with the spawning of mysid shrimp in the Galveston estuaries. Therefore, small mysids with a total length of about 2.0 mm (Fig. 4B) were abundantly supplied. This was particularly important since small mysids swim more frequently in the water column than do adults. Young mysid hatchlings were given as food by day 12 in L.O. 1981 and immediately in L.O. 1982 (Fig. 3). Small mysids distribute themselves more evenly in the culture tanks and are easier for hatchlings to capture. *Palaemonetes* spp. were fed to juvenile and adult squid (Fig. 3). Shrimp ranged in size from 2.0 to 25.0 mm. They were graded by size and fed based on size and availability. Daily siphoned remains indicated that only the abdominal flesh was consumed, with the thorax and carapace discarded.

Fish were generally used for juvenile or older squid. However, fertilized red drum eggs were available in L.O. 1981, and larvae up to 13-d old (Fig. 4E) were given to the hatchlings. In the two experiments, a total of over 14 fish species of 10 families were fed (Table 2). To determine the diet preference for fish species, the actual consumption of fish (i.e., total weight of fish put in tank minus total weight of fish remains) was compared for a total of 5 kg fish fed in L.O. 1982 (Fig. 6). The cyprinodont fish were most preferred (consumption of 83%). Only small *Fundulus* spp., smaller than 31 mm (Cyprinidontidae), were fed because large *Fun-*

TABLE 1.—The mean density of squid and food organisms per liter of culture water from days 0-30 and 30-59.

		Day 0-30			Day 30-59		
Exp. No.	Initial hatchling population	Squid No./L	Food organisms No./L	Ratio of food organisms to squid	Squid No./L	Food organisms No./L	Ratio of food organisms to squid
L.O. 1980	864	0.46	14.2	30:1	0.35	9.4	26:1
L.O. 1981	2,061	0.93	24.0	25:1	0.54	12.4	23:1
L.O. 1982	1,704	0.27	14.6	54:1	0.14	5.6	40:1

1981 EXPER


CT
°C
19
18
17
16
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14
CT
RW
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DAYS

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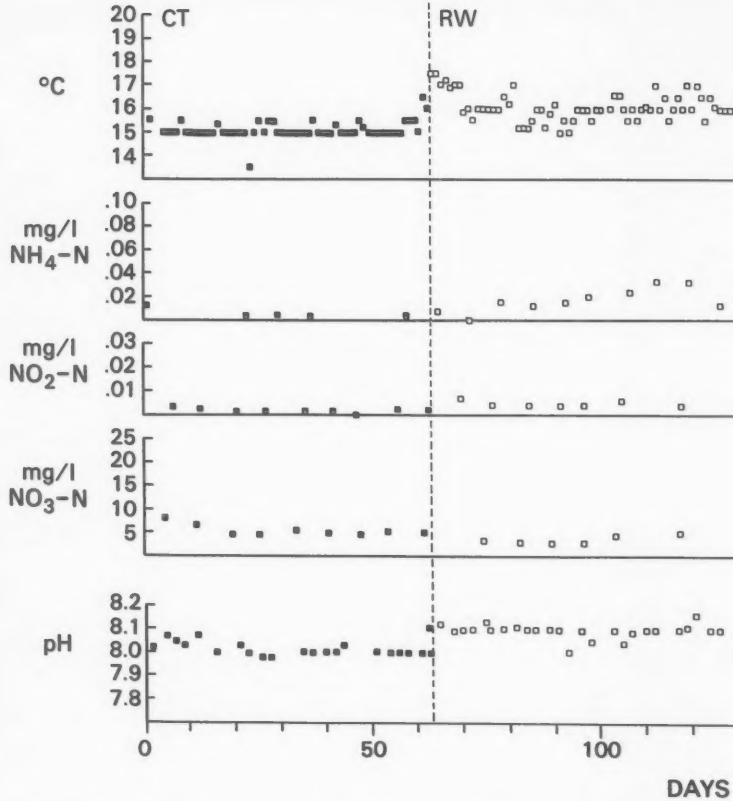
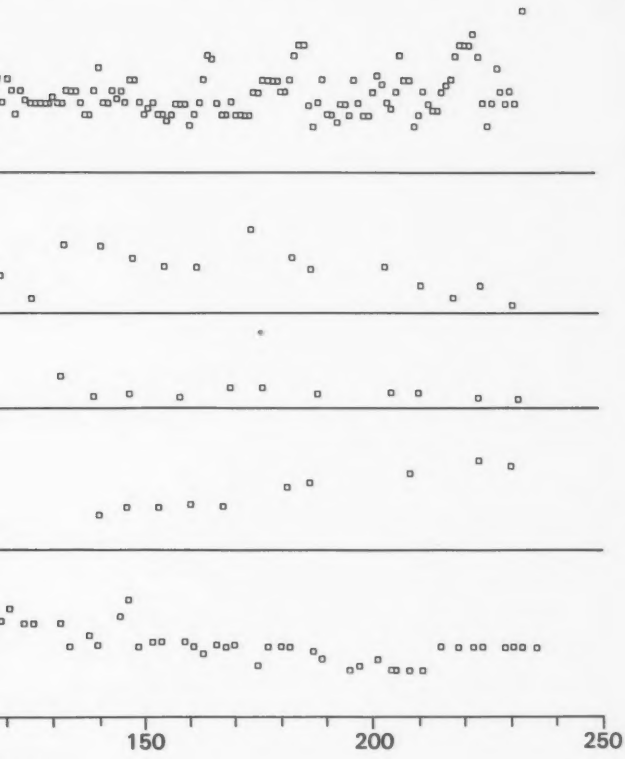


FIGURE 2.—Water quality measurements in CT (circular tank) and RW (raceway) systems throughout the life cycle (L.O. 1981 and 1982). Some squid in L.O. 1981 were kept in the C tom t

RIMENT



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the CT system (see top temperatures) while others were moved to the RW system (bottom temperatures).

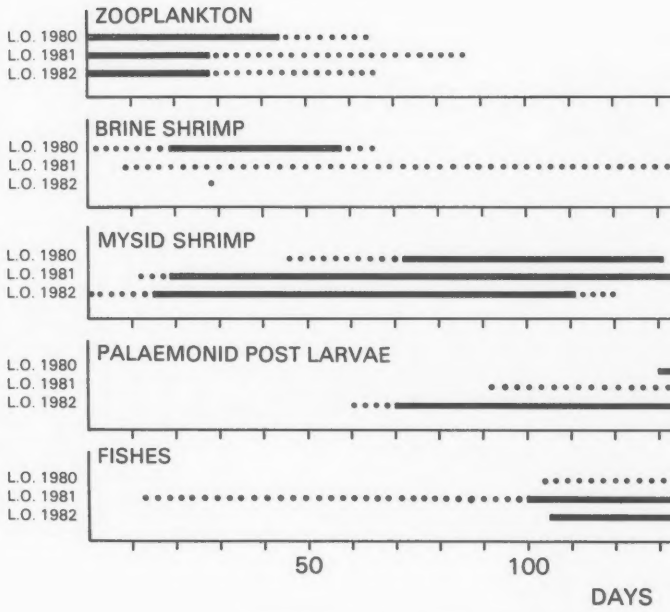


FIGURE 3.—Comparative use of food organisms fed to *Lolig*

o *Loligo opalescens* during three culture experiments.

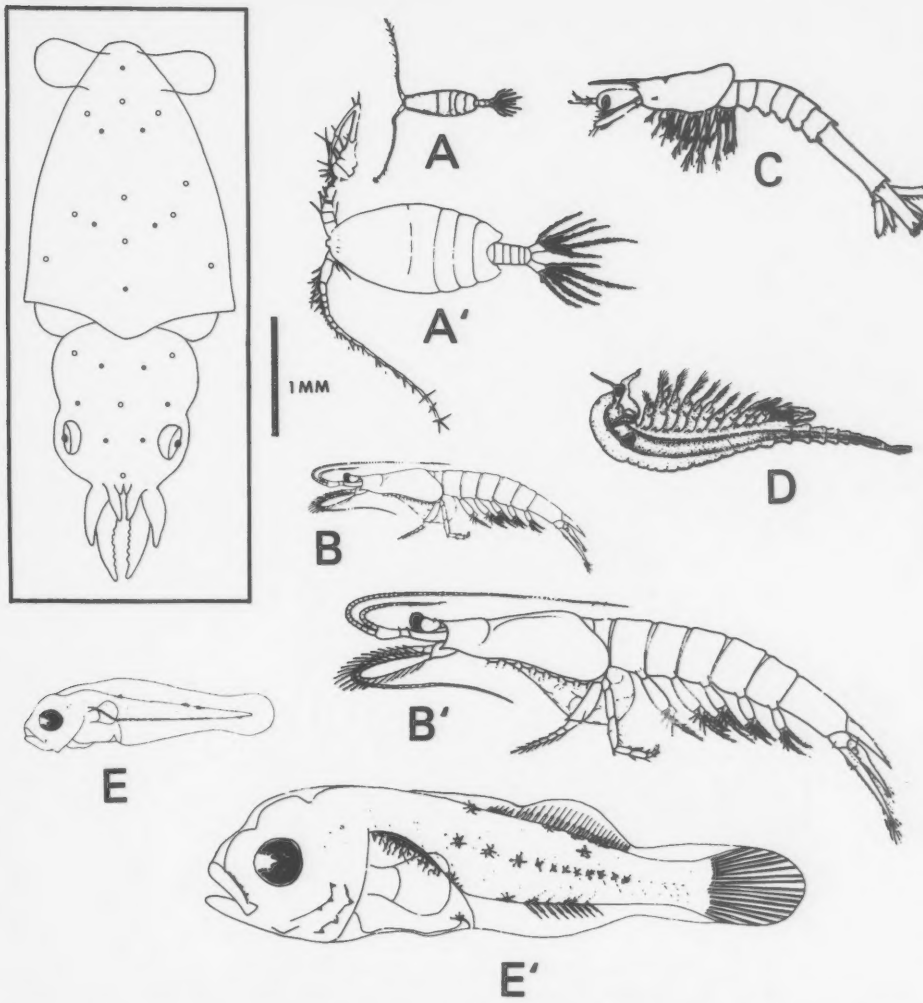


FIGURE 4.—Size relationship of hatchling *Loligo opalescens* and various food organisms fed squid for the first 30-d posthatching. A, copepod *Acartia tonsa*; A', copepod *Labidocera aestiva*. B, hatchling *Mysidopsis almyra*; B', adult *M. almyra*. C, mysis stage of *Penaeus* spp. D, adult *Artemia salina*. E, 1-d-old larva of red drum *Sciaenops ocellatus*, E', 13-d-old larva of *S. ocellatus*.

dulus spp. competed with the squid for crustaceans in the tank. Uneaten mullet (Mugilidae) accumulated to form small schools, that the squid would not approach or feed upon as readily as fish that swam individually. Squid consumed 44% of the mullet even though the amount fed was equal to amounts of Poecilidae and Sciaenidae, which were consumed more (72% and 68%, respectively). The food remains indicated that the squid ate only the flesh of fish, leaving the head and vertebrae.

Figure 7 gives the estimated daily group feeding rate (L.O. 1981) based upon the daily biomass of squid and the daily food consumption from day 108 to day 232. Daily group feeding rate averaged 14.9% (range 4-29%). Squid biomass reached a maximum on day 183 and continued high for 11 d before the

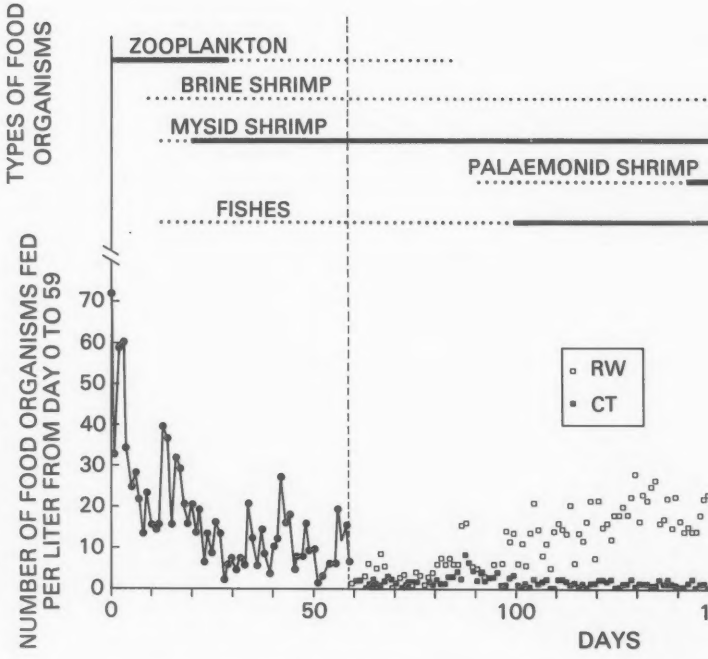


FIGURE 5.—Types, quantities and densities of food organisms fed daily in experime

periment L.O. 1981. Vertical line represents the culture day 59.

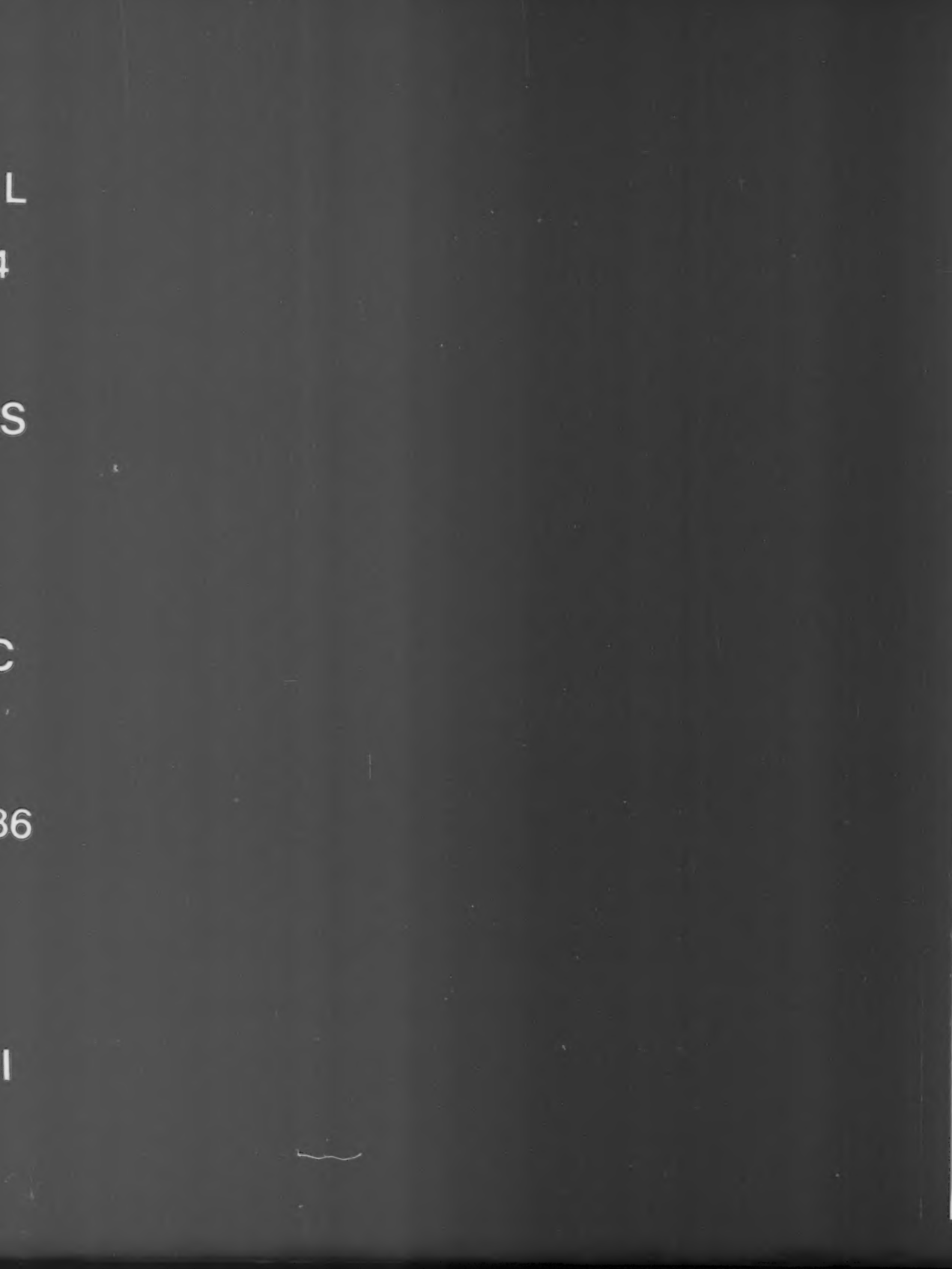


TABLE 2.—Fish species and size range given as food in all three experiments.

Family and species	Size (TL in mm)	L.O. experiment 1980	1981	1982
Family: Clupeidae				
Brevoortia spp.	15.0-31.0	—	—	X
Family: Engraulididae				
Anchoa mitchilli (Valenciennes)	20.0-25.0	—	—	X
Family: Cyprinodontidae				
Adinia xenica	—	—	—	X
Cyprinodon variegatus Lacepede	10.0-28.0	X	X	X
Fundulus spp.	15.0-31.0	X	X	X
Family: Poeciliidae				
Gambusia affinis (Baird and Girard)	12.0-28.0	X	X	X
Poecilia latipinna (Lesueur)	22.0-41.0	X	X	X
Family: Atherinidae				
Menidia beryllina (Cope)	18.0-52.0	X	X	X
Family: Carangidae				
Hemicaranx amblyrhynchus (Cuvier)	—	—	—	—
Family: Gerreidae				
Eucinostomus gula (Quoy and Gaimard)	—	—	X	X
Family: Sparidae				
Lagodon rhomboides (Linnaeus)	—	—	X	X
Family: Sciaenidae[1]				
Sciaenops ocellatus (Linnaeus)	1.5-14.5	—	X	X
Pogonias cromis (Linnaeus)	10.0-15.0	—	X	X
Family: Mugilidae				
Mugil spp.	18.0-38.0	X	X	X

[1]There were about six more species of Sciaenidae; minority species were not identified.

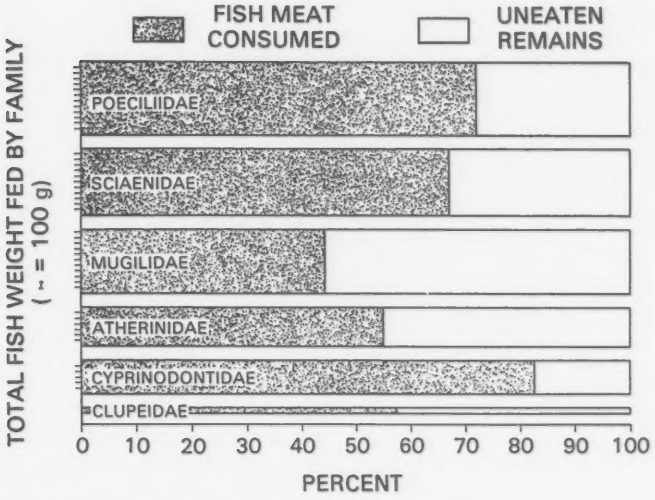


FIGURE 6.—Food preference for fishes by squid in experiment L.O. 1982. Total fish weight fed to the squid was 5.0 kg.

initiation of spawning; biomass then decreased because of the mortality accompanying spawning. Squid in L.O. 1982 were fed ad libitum and daily group feeding rates could not be determined. However, the average group feeding rate calculated weekly for L.O. 1982 allowed an estimate of 18.0% for the daily feeding rate.

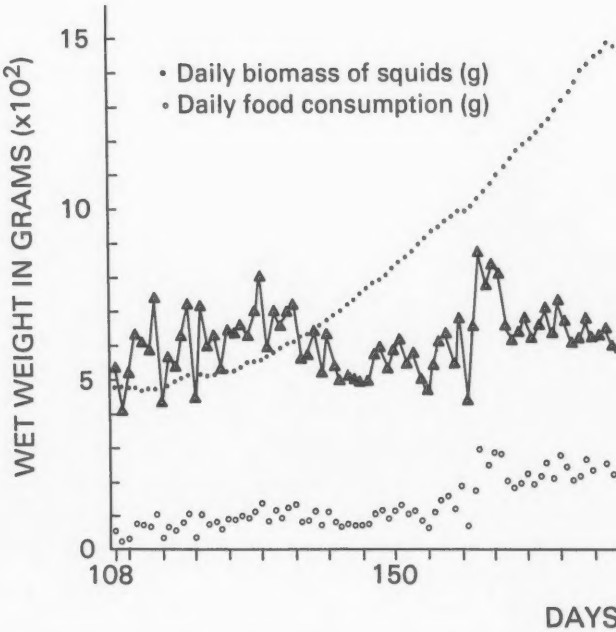
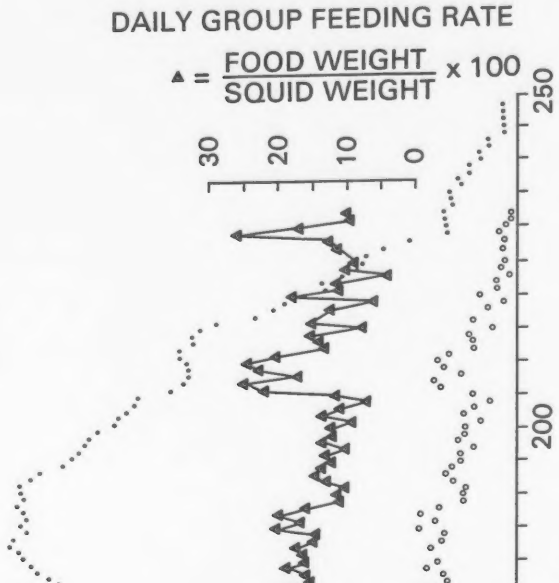


FIGURE 7.—Analysis of the daily group feeding rate of subadult and adult *Loligo op*



igo opalescens in the RW system from day 108 to 248 in experiment L.O. 1981.

Growth

Figure 8 illustrates growth data through the life cycle for both experiments. At hatching, *Loligo opalescens* has a mean mantle length of 2.7 mm, a wet weight of 0.001 g, and has approximately 100 chromatophores on its body. In L.O. 1981, the largest reared squid was a male of 113 mm ML and 58 g. In L.O. 1982, the largest reared squid was a female of 116 mm ML and 63 g. Mean sizes for adults from the two experiments were 87 mm ML ($S\bar{x}$ = 2.7) and 23.8 g ($S\bar{x}$ = 1.9) for 35 males, and 83 mm ML ($S\bar{x}$ = 1.9) and 21.2 g ($S\bar{x}$ = 1.5) for 58 females.

Growth equations for the squid in L.O. 1981 clearly describe two separate phases of growth. The mantle length of squid cultured in the CT system (days 1-56) increased at an exponential rate ($ML = 2.121\ e^{0.02398t}$; $r^2 = 0.92$) or 2.4% increase per day, while those cultured in the RW system (days 56-248) grew logarithmically ($ML = 0.2884\ t^{1.495}$; $r^2 = 0.97$). Weights were only measured on squid from the RW

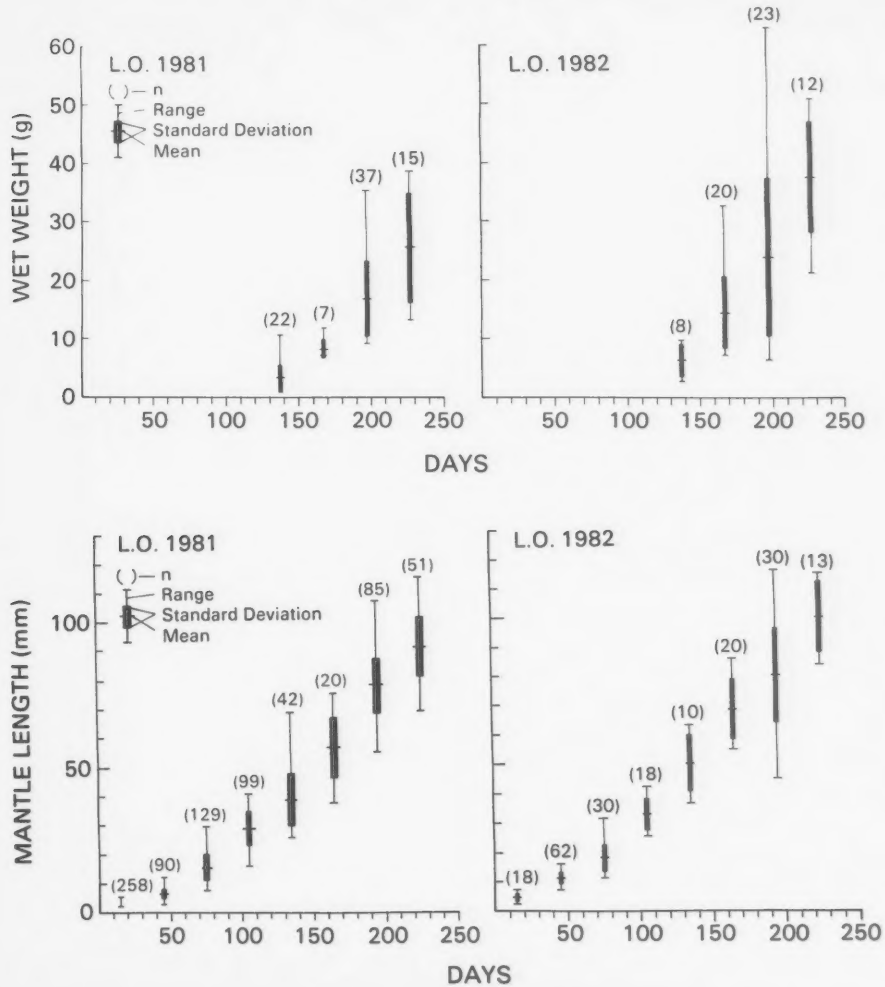


FIGURE 8.—Comparison of growth (wet body weight and mantle length) in experiments L.O. 1981 and L.O. 1982.

system (days 108-248) and the growth curve showed a logarithmic increase ($W = 6.283 \times 10^{-7}\, t^{3.660}$; $r^2 = 0.92$). Hence, younger squid grew at an exponential rate and growth slowed to a logarithmic rate in older squid.

Squid exhibited fast exponential growth for the first 2 mo in L.O. 1982 and slower logarithmic growth thereafter (Fig. 9). Wet weight data from live animals in L.O. 1982 indicated a mean growth rate of 8.35% increase in body weight per day for the first 2 mo. Mantle length increased 3.19%/day or the equivalent of 8 mm/month. The squid were doubling their weight every 8 d and doubling their length every 21 d. Growth rates declined from 5.6%/day WW at day 60 (and 2.2%/day mm ML) to 1.6%/day WW (and 0.63%/day mm ML) at day 240.

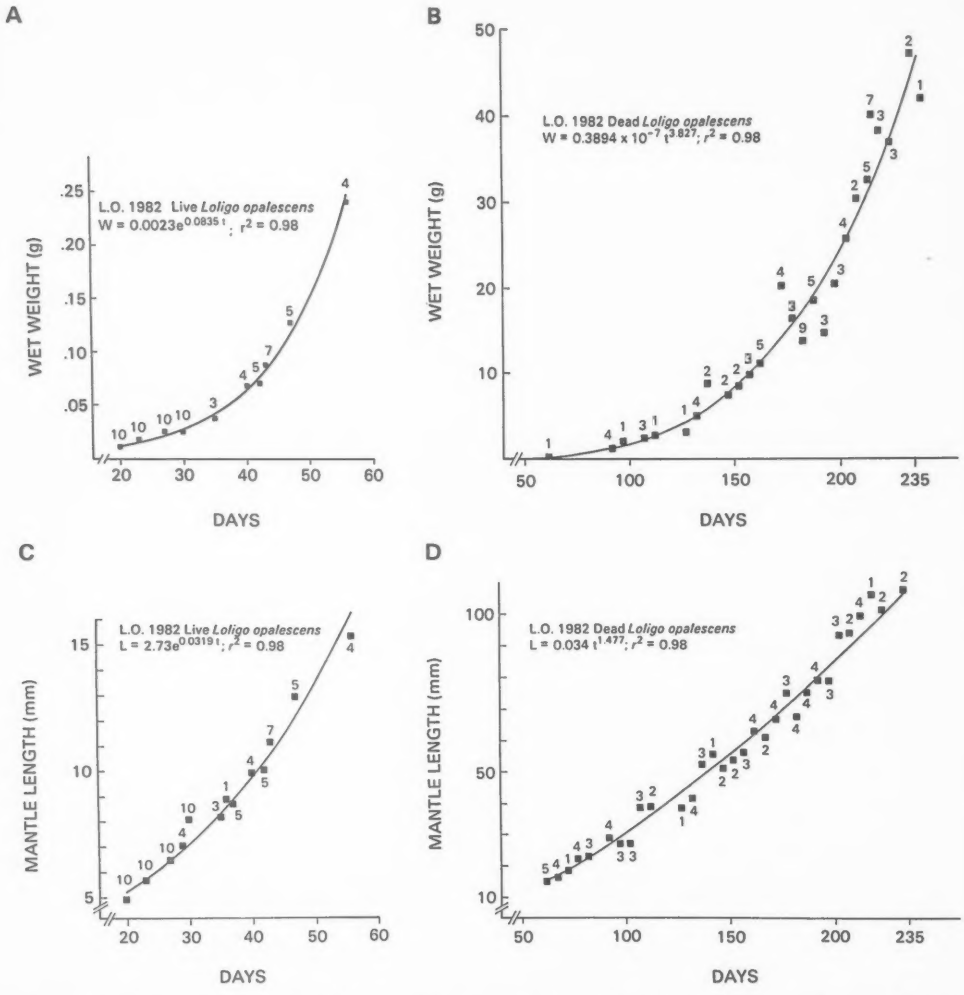


FIGURE 9.—Early exponential growth of *Loligo opalescens* in experiment L.O. 1982: A, Live wet weight, illustrating exponential growth through day 60. B, Dead wet weight, illustrating logarithmic growth from day 60 to maturity. C, Live mantle length measurements, showing exponential growth as in A. D, Dead mantle length measurements, showing logarithmic growth to maturity as in B. Numbers above rectangles indicate actual number of squid measured for that mean.

Mean growth was 16 mm/month for this period. Doubling times for weight increased from 12 d at day 60 to 42 d at day 240, and for length from 31 d at day 60 to 109 d at day 240.

The length-weight relationships of squid in L.O. 1981 and 1982 are illustrated in Figure 10 and are compared with data on wild squid (Fields 1965). The slopes of the curves are slightly higher in laboratory-reared animals, indicating that these squid are heavier per unit length than wild squid. Table 3 illustrates differences in predicted weights for representative mantle lengths from L.O. 1982 data versus Fields' (1965) data. The length-weight relationship for males vs. females in L.O. 1981 is shown in Figure 11; no significant differences between sexes were detected ($P > 0.05$).

Statoliths from 55 early hatchlings (L.O. 1982) aged 21 to 79 d (±5 d) were examined to correlate statolith ring numbers with the age of individual squid (Fig. 12). The linear relationship between the number of rings (R) and the age in days (D) for 43 statoliths aged 21 to 65 d was $R = -7.24 + 1.13\ D$, with an r^2 value of 0.90. Counts of rings differed from the actual age by an average of ±4.2 d (range −12 to +8 d).

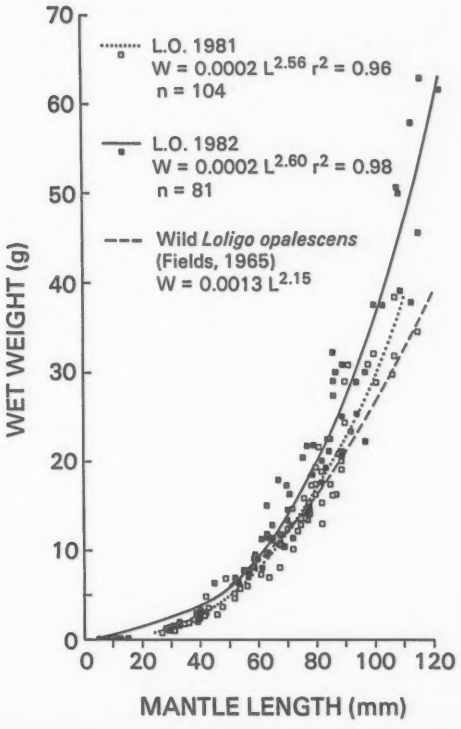


FIGURE 10.—Comparison of length-weight relationship of squid cultured in L.O. 1981 and 1982, and squid collected in the field at Monterey Bay, CA by Fields (1965).

TABLE 3.—Examples of length-weight differences between L.O. 1982 and the data of Fields (1965). Reference Figure 10. ML = mantle length; WW = wet weight.

ML (mm):	25	50	75	100	125
L.O. 1982: WW (g)	0.86	5.22	15.00	31.70	56.60
Fields (1965): WW (g)	1.31	5.80	13.90	25.90	41.90

Survival

Figure 13 compares survival in the two experiments. The longest lived squid were 248 d in L.O. 1981 and 235 d in L.O. 1982. Survival dropped below 50% on day 15 in L.O. 1981 and on day 2 in L.O. 1982. In L.O. 1982, the early rapid population reduction was due to the removal of newly hatched squid for a different experiment. Mortality rates slowed after the early heavy population reduction; 10% survival occurred on day 120 in L.O. 1981 and on day 49 in L.O. 1982. In all cases, mortality gradually slowed after 60- to 70-d posthatching. Survival reduction after day 180 in both experiments was considered to be related to spawning (Figs. 13A, B).

In L.O. 1981 experiment (Fig. 13A), 50% survival of 391 squid transferred to the large RW system occurred at day 114, but at day 84 for the 129 squid left in the same small CT system. For example, 10 d after transfer the squid in the CT system had 30% mortality whereas those in the RW system experienced only 20% mortality. Thus, transferring squid at about 60 d gave better results by reducing the mortality from fin and skin damage that accrues in the smaller CT system.

In the middle of L.O. 1981 (day 108) cannibalism was observed. The fins and/or posterior mantle were clearly eaten in some squid; these squid differed from those that died from fin damage or from scraping on the bottom of the tank since the latter developed lesions near the tip of the mantle (Fig. 14). From days 108 to 206 there were 16 partly eaten squid in the RW system (7% of the population on day 108), compared with two squid (of 10 total) in the CT system between days 157 and 172. Slightly higher levels of cannibalism (19% between days 97 and 191) were observed in L.O. 1982.

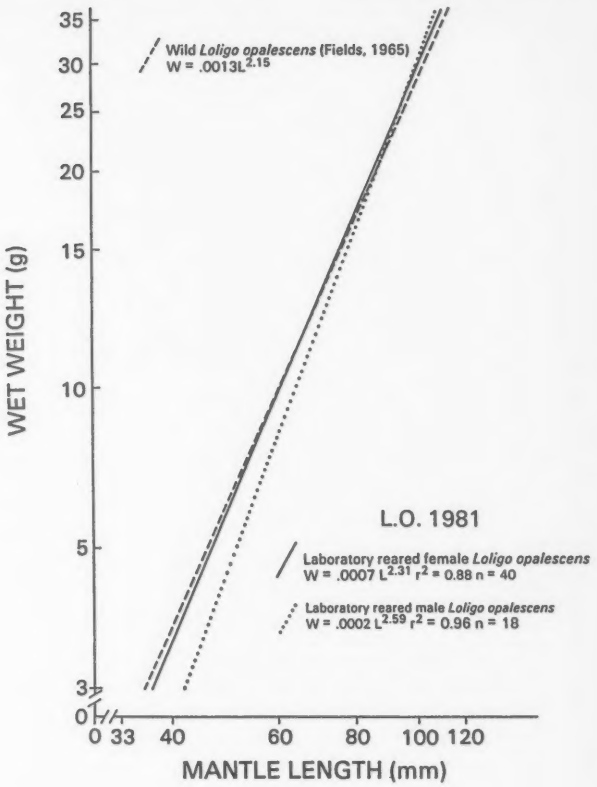


FIGURE 11.—Length-weight relationship of males versus females in L.O. 1981, compared with the data of Fields (1965).

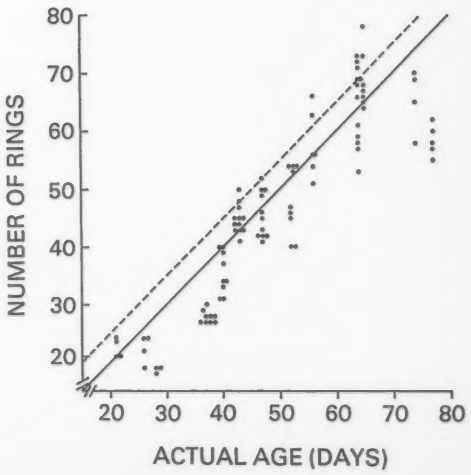


FIGURE 12.—Increase in statolith rings with age (L.O. 1982). Closed circles represent ring counts of 55 statoliths from *L. opalescens* of known-age (21-79 d). Each statolith was counted twice from different photographs. Unclear exposures (16) were not counted. The solid line represents a linear relationship of age and ring numbers. The space between the solid and dashed lines reflects the 5 d of hatching.

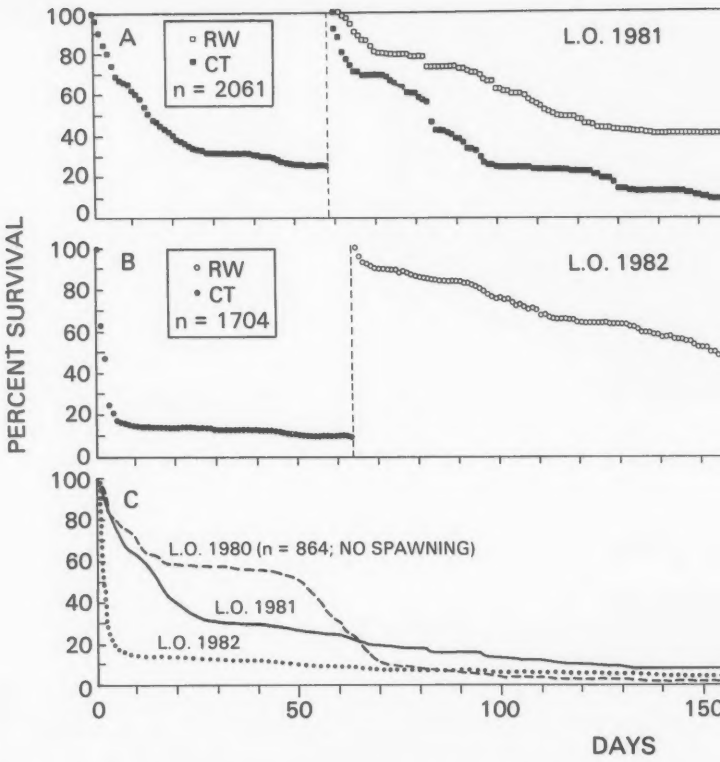


FIGURE 13.—Comparison of daily percent survival and spawning (number of egg capsules in inverted histogram) activity of *Loligo opalescens* in three culture experiments. A, on day 59 (vertical dashed line), 391 squid were transferred to the 10,000 L RW system for the rest of the experiment; the remaining 129 squid were cultured in the CT system. Survival thereafter was calculated as a percent of the number of squid alive on day 5 to the RW sy egg capsules from all three each experim

n day 59 in each tank system. B, The cultured 147 squid were transferred RW system on day 63. Spawning began early on day 173. A maximum of 27 psules were spawned in 1 d. C, Comparison of the daily percent survival data l three *L. opalescens* culture experiments. CT and RW data were pooled for xperiment for this analysis.

Other causes of injury and death in the later part of RW culture were 1) swimming into the water intake pipes, 2) jetting out of the water and hitting the bottom of the polystyrene tank covers, and 3) colliding occasionally with the walls and slowly accruing fin damage. The resulting abrasions on the body and fins (Fig. 14) were probably the main factor influencing mortality after about 60 d of culture.

1 or 2 d. They usually had some obvious skin damage and were probably unable to maintain disciplined swimming with the school.

Sexual Maturation, Mating, and Egg Laying

In L.O. 1981, the first signs of sexual maturation were when chromatophore patterns associated with

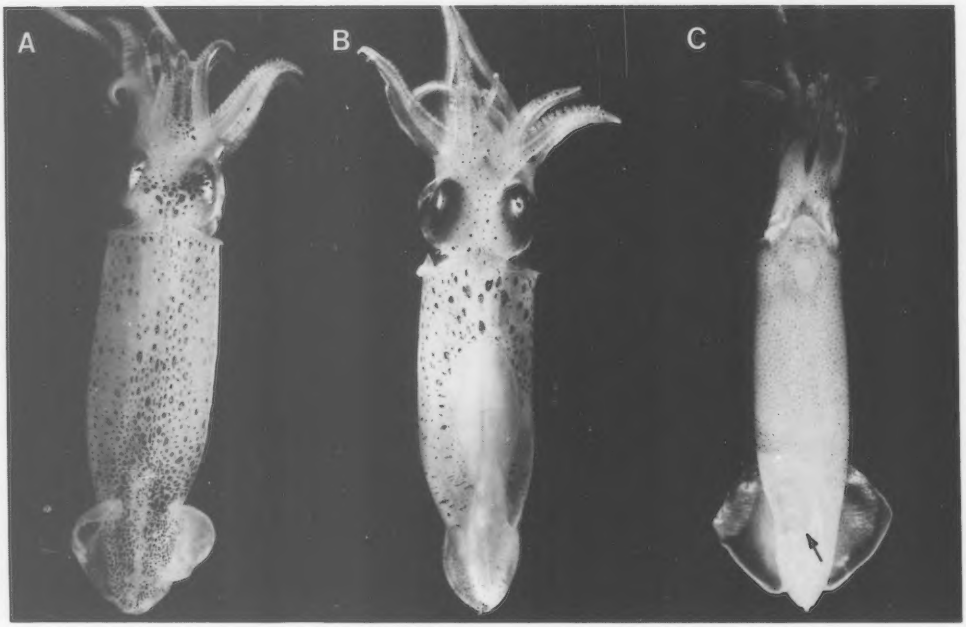


FIGURE 14.—Fin and skin damage that resulted in mortality of cultured squid. A, Epidermis and dermis missing on periphery of fins, with fin margin thickened from scar tissue. B, More extreme case with damage extended to mantle. C, Excessive skin damage on ventral mantle caused by scrapping the tank bottom. A hole (arrow) was produced in the mantle wall and prevented jet-propulsed swimming.

Schooling Behavior

The squid were able to hold a swimming position in the tank between days 41 and 44 in both L.O. 1981 and 1982, corresponding to a mantle length of about 10 mm. In the early phase of RW culture in L.O. 1981 and 1982, squid swam in two or three loose groups throughout the RW. Later, they schooled together at both ends. The reasons for this behavior are unknown, but it may have been related to lower illumination levels at the RW ends or to the well-aerated seawater entering the RW at these points. Individuals not schooling were often found dead in

courting were observed in males. On day 174 two males showed the "Shaded testis" component of patterning similar to that described in *Loligo plei* (Hanlon 1982). Later, other chromatic components of patterns seen in mature males of *Loligo plei* were observed: faint, lateral stripes on the mantle ("Lateral flame"); a discontinuous suture line along the fin margin ("Stitch work fins"); a clear area in the dorsal portion of the mantle above the testis ("Accentuated testis").

Maturation and spawning occurred earlier in L.O. 1982 than L.O. 1981 (Fig. 13). The penis was first recognizable in a 100-d-old male (25 mm ML) and

the nidamental gland was observed in a 101-d-old female (23 mm ML) in L.O. 1981. The penis was first recognizable in a 93-d-old male (29 mm ML, 1.15 g WW), and the nidamental gland was observed in a 92-d-old female (33 mm ML, 1.71 g WW) in L.O. 1982. Figure 15 shows that females become mature at approximately 60 mm ML. This maturation index is based upon reports by Hixon (1980a) and Macy (1982) in which the ratio of nidamental gland length to mantle length is >0.20. Squid this size could produce fully formed egg capsules. The smallest male with spermatophores was 71 mm ML in L.O. 1982.

In L.O. 1981, first mating activity was observed on day 193. A pair was swimming together, a second male interrupted, and a third male grasped the female in the midmantle area but she jetted away. On day 197 another pair was swimming together at the end of the RW and a brief head-to-head mating was observed. They separated for about 1 min, then the male grabbed the female by the arms for a second time. Drew (1911) illustrated this copulating position in *Loligo pealei*. A second mating position was observed on day 226. A male grasped a female's mantle one-third of the way from the posterior tip of the mantle, then he gradually moved to the female's head near the mantle opening and then let go. This was done very swiftly and it was impossible to see if a spermatophore was passed. Freshly dead females had spermatophores attached around the sperm receptacle below the mouth after head-to-head matings. Mating activity was not as closely monitored in L.O. 1982, but first observations were several weeks earlier (before day 175).

Spawning started on day 196 and lasted till day 239 in L.O. 1981. Of 151 egg capsules, 24 (16%) were unfertilized (Table 4). Squid kept in the CT system (3°C higher temperature from day 125) spawned first on day 185, 11 d earlier than the RW system, but none were fertile. Spawning occurred earlier in L.O. 1982, beginning day 175 and ending day 222. All of the 199 spawned capsules were infertile. The maximum number of spawned capsules in a single day was 27 on day 203 (Fig. 13B). Most eggs were collected in the morning indicating that spawning

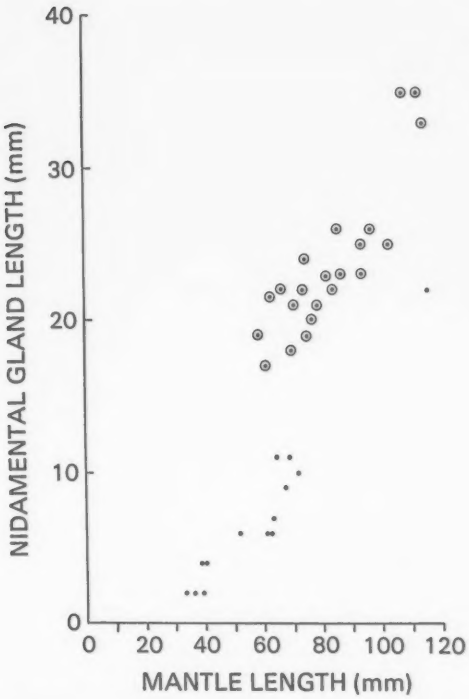


FIGURE 15.—Maturation index for females from pooled data of L.O. 1981 and 1982. Dots with circles indicate sexually mature females in which the ratio of nidamental gland length to mantle length is >0.20. See text.

TABLE 4.—Spawning date and number of egg capsules spawned in the raceway system (L.O. 1981).

Month/ day	Age/ day	Capsules spawned	Capsules without eggs
05/01	196	3	0
05/03	198	2	0
05/04	199	5	0
05/05	200	6	0
05/06	201	1	0
05/08	203	1	0
05/09	204	6	0
05/10	205	5	0
05/16	211	5	1
05/17	212	8	0
05/19	214	5	2
05/20	215	3	3
05/21	216	17	8
05/22	217	17	2
05/23	218	14	0
05/24	219	7	0
05/25	220	3	0
05/26	221	6	0
05/27	222	3	0
05/28	223	7	2
05/29	224	6	1
05/30	225	1	0
05/31	226	2	1
06/02	228	5	2
06/03	229	4	2
06/11	237	5	0
06/12	238	4	0
	Total	151	24 (16%)

took place mainly at night, but some individuals spawned during the day. Egg capsules in the early portion of the spawning period were small, with a length of 2.2 to 4.7 cm when laid. Superficially there were no differences with normal capsules, but usually the early ones contained only a few eggs while a few had none. Typical newly laid egg capsules were between 6.0 and 9.0 cm and contained an average of 156 eggs (range 107-199). These egg capsules were normal in length and egg number compared with *L. opalescens* in nature (Hixon 1983).

A large number of typical egg capsules were incubated and a normal second generation hatched. The average mantle length of second generation hatchlings was 2.3 mm ML (range 1.9-2.7 mm ML, n = 13). This was smaller compared with first generation hatchlings (average 2.7 mm ML) but there was no difficulty in rearing them on copepods for 10 d. Since initial survival was confirmed, further rearing ceased.

In L.O. 1982, three patches of artificial egg capsules made of silicon glue were placed on the bottom of the RW tank to stimulate spawning. The squid spawned 15 fertilized egg capsules around the artificial capsules (Fig. 16).

DISCUSSION

Water Quality and System Design

Water quality was consistently good throughout both experiments and was probably a major contributor to culture success. The CT systems were particularly clean (Fig. 2) because the water volume was relatively large for the small biomass of animals. In the large RW system, water quality changed only slightly when the biomass of squid and food organisms reached its maximum from approximately days 150 to 220 (Figs. 2, 5, 7). The highest total biomass level was 1,706 g between days 180 and 190 in L.O. 1981, which is equivalent to approximately 155 g/m^3 of water. At this point, the nitrate-nitrogen level reached 23 mg/L, which is still low [Spotte (1979a) gave a conservative safe level of 20 mg/L for most marine organisms]. Ammonia-nitrogen and nitrite-nitrogen levels always stayed below the recommended safe level of 0.1 mg/L (Spotte 1979a) in both experiments. We know from our recent unpublished data that a drop in pH (which accompanies nitrogen level increase; Hirayama 1966) is more dangerous to squid; therefore, addition of sodium bicarbonate was necessary to keep the pH near 8.0. Several improvements in system design helped improve water quality over our *L. opalescens* experiment in 1980 (Yang et al. 1983a), when nitrite-nitrogen reached 1.22 mg/L and nitrate-nitrogen reached 39.20 mg/L. These included increased culture water depth and volume in the RW (5,990 to 8,610 L), increased number of protein skimmers from 2 to 5 and generally more oyster shell substrate area for increased biological filtration. Furthermore, regular addition of trace metals assured high levels since losses occur through foam fractionation in protein skimmers (Spotte 1979b) and metabolism of filter bed bacteria, squid, and food organisms.

Growth and Survival

Growth in *L. opalescens* is very fast (Figs. 8, 9) and conforms to a general trend among cephalopods in which the early life cycle is characterized by rapid exponential growth, followed by slower logarithmic growth until reproduction and death (Boyle 1983; Forsythe and Van Heukelem in press).

Egg development is temperature-dependent and takes 19 to 25 d at 16.5°C (Fields 1965), 27 to 30 d at 15°C (L.O. 1981, this report) and 30 to 35 d at 13.6°C (McGowan 1954). Hatching success was high, and young squid survived several days on internal yolk. Many squid will feed before internal yolk is absorbed (Boletzky 1975). The young will feed on a variety and wide size range of crustaceans and fishes (Fig. 4). Zooplankton, but especially copepods, are readily attacked and eaten by very young squid. It is noteworthy that relatively large mysids could be fed successfully to hatchlings within the first week (Fig. 3: L.O. 1982) and for 3 to 4 mo thereafter as a primary food. Mysids are easier to collect and acclimate to laboratory conditions and are thus attractive to the culturist for pragmatic reasons. *Loligo opalescens* hatchlings (2.3-2.8 mm ML) are much larger than those of *L. pealei* (1.7 mm ML) or *L. plei* (1.6 mm ML) (McConathy et al. 1980) and are consequently easier to rear because larger food organisms can be used immediately. Larval fish were attractive to young squid but are difficult to provide.

Major mortality occurred within 10 d posthatching. Although high food densities and variety were provided (Tables 1, 2; Figs. 3, 4, 5), many squid appeared to have difficulty making the transition from passive yolk absorption to active feeding on live organisms. A learning process may be involved, because capturing copepods was initially difficult (squid have been observed to miss 40 times consecutively) and improved when squid attacked from behind. Past experience (cf., Yang et al., 1983a) suggested that increasing food abundance relative to

FIGURE 16.—Fertilized egg capsules laid at the base of artificial silicon egg capsules (erected).

squid abundance would enhance survival, but no change has been observed. Further experimentation is required, but a central question is whether many squid are genetically unfit to survive or whether we have not yet provided the proper foods and environment for good survival. Although the former prospect seems unlikely from the evolutionary viewpoint, our experimental design has certainly promoted outstanding growth in surviving squid.

With the growth data from live squid in L.O. 1982, we confirmed that squid grow exponentially both by weight and length during the first 2 months (Fig. 9). Weight increases at a rate of 8.35% body weight/day (doubling their weight every 8 d) and this compares very favorably with octopods (4-7%), other squid (5-7%), and cuttlefishes (5-12%) (Forsythe and Van Heukelem in press). Logarithmic growth during the rest of the life cycle also conforms generally to other cephalopods, except that some cephalopods have a longer exponential growth period up to one-half their life cycle (Forsythe and Van Heukelem in press). The length-weight relationship (Figs. 10, 11) generally conforms to those of wild-caught squid, but indicates that laboratory-reared squid weigh more per unit length (Table 3), possibly, as a result of reduced swimming. The slopes of the lines (all <3.0) indicate allometric growth (Forsythe and Van Heukelem in press). The estimated feeding rates of 18.0% body weight/day (days 121-176) in L.O. 1982 and 14.9% (days 108-230) in L.O. 1981 compare well with the estimate of 14.4% (on a dry weight basis) for *L. opalescens* of a similar size in the natural population (Karpov and Cailliet 1978). Younger *L. opalescens* (48-56 d) fed on *Artemia* were estimated by Hurley (1976) to feed at rates of 36 to 80%/day (dry weight). Another loliginid squid, *Sepioteuthis sepioidea*, had feeding rates of 20 to 25% (wet weight) between days 70 and 105 (La Roe 1971). Other squids of similar size show comparable rates: *Loligo plei*, 10 to 18% (Hanlon et al. 1983); *L. pealei*, ca. 11% (Macy 1980); *Illex illecebrosus*, ca. 10% (Hirtle et al. 1981); and *Todarodes pacificus*, ca. 24% (Soichi 1976).

Maximal survival and size in our three major experiments were L.O. 1980 - 233 d, 77 mm ML (Yang et al. 1983a); L.O. 1981 - 248 d, 113 mm ML; L.O. 1982 - 235 d, 116 mm ML. Figure 13 illustrates survival throughout these experiments and shows that there was a long, steady mortality after the initial high mortality of the first 2 wk. Once in the RW systems (i.e., after 2 mo) most mortality was attributed to fin and skin damage (Hulet et al. 1979; Fig. 14) that accrued slowly from colliding with the sides of the tank. The painted designs on the walls were clearly helpful in reducing wall collisions but damage over time was lethal in many squid. Cannibalism accounted for a minor number of deaths (ca. 7-10%) Most mortality after day 170 in L.O. 1981 and L.O. 1982 was due to 1) sexual maturation and spawning and 2) an unusual situation where fully mature females scraped the bottom of the tank often enough to wear a large lesion through the ventral mantle (Fig. 14C).

It should be noted that survival rate was greater where large tanks such as the RW were used. In L.O. 1981 (Fig. 13A), 50% survival of squid left in the smaller CT system occurred only on day 84 compared with day 114 for those transferred to the RW.

In summary, growth was excellent, indicating that estuarine foods were sufficient and that system design and water quality were conducive to growth, especially in the first 2 mo. Survival was good from the historical perspective (cf., Arnold et al. 1974; Yang et al. 1983b) but rather poor from the production standpoint. A recent hypothesis concerning temperature effects on growth (O'Dor and Wells in press) indicates that higher temperature in the first half of the life cycle and lower temperature in the latter half may enhance growth and survival of laboratory-reared squid. In future work it would be desirable to enhance growth during the latter half of the life cycle and to provide an environment in which somatic growth continues for a longer period before sexual maturation occurs.

Behavior

Squid are generally sensitive laboratory animals, responding very quickly with their sophisticated sensory systems to any fast environmental change. They habituate to many daily disturbances in the tank system (e.g., tank cleaning, etc.) provided everything is done slowly. Later in the life cycle they become slightly less sensitive.

Hatchlings were positively phototaxic and often swam at the water surface. In nature, young squid have been caught mainly by plankton nets mounted on a sled and towed along the bottom (Recksiek and Kashiwada 1979). It is not possible at this time to explain the movements of hatchlings in nature based upon laboratory observations of positive phototaxis.

A key component in feeding behavior was movement by the prey, regardless of the size or age of the squid or food organisms. Young squid preferred copepods but ate a variety and a very wide size range of organisms (Fig. 4). In general, the squid preferred crustaceans over fish, but the relatively

restricted diet offered to them may have influenced that. Fields (1965) and Karpov and Cailliet (1978) agreed that *L. opalescens* adults prefer fish over crustaceans but there was no clear-cut preference in younger squid. It is clear from laboratory observations that squid learned to associate certain events with feeding (e.g., opening the tank top), and the general level of activity increased markedly during these periods. We were also able to stimulate feeding in the CT systems by dimming and brightening the lights to attract the planktonic food organisms into the water column near the squid.

Schooling behavior was correlated with size. Larger body size and growth of the fins were required before squid could swim in place against a current; this occurred at about 10 mm ML (41-44 d in L.O. 1981 and 1982). Hurley (1976) reported that *L. opalescens* 4 to 5 mm ML could briefly form loose schools when disturbed, but this may have been in static water. At 15 mm ML, *L. opalescens* were powerful enough to form distinct schools (Yang et al. 1983a), indicating the size at which one could expect schooling to appear in nature. How and why squid begin schooling in nature has not been investigated.

Cannibalism was not seen in L.O. 1980 (Yang et al. 1980b, 1983a) and accounted for 7 to 19% of mortalities in experiments L.O. 1981 and 1982. Lack of food did not precipitate this behavior. On the spawning grounds in Monterey, CA, mature squid often have cephalopod remains in their stomachs (Loukashkin 1977; Karpov and Cailliet 1978); in one case as many as 75% of males had squid remains in their stomachs (Fields 1965). This could be a behavioral response to overcrowding (Fields 1965) or to restrict prey organisms on the spawning grounds. We anticipate that cannibalism in tanks would be a significant problem only during prolonged food shortage or if squid of a very wide size range were in the same system (cf., Hanlon et al. 1983).

Body patterning was not studied in great detail but several observations are noteworthy. Young animals are capable only of simple chromatic expression such as "All dark" or "Clear". When excited, *L. opalescens* of all sizes show some degree of darkening; this is similar to other loliginid squids (cf., Hanlon 1982; Hanlon et al. 1983). By the time the squid are approximately 80 to 100 mm ML they can show a repertoire that includes about a dozen chromatic components of patterning (e.g., Dark arm tips, Ring on the mantle, etc.). This places *L. opalescens* in a category of rather simple patterning, making it comparable to *L. pealei* and *L. vulgaris*, slightly more complex than *Lolliguncula brevis* (Dubas et al. 1986), but simpler than *Loligo plei* (Hanlon 1982; Hanlon et al. 1983). Further analysis is warranted because much behavior is expressed through patterning and may yield important behavioral clues.

Social behavior was first manifest in schooling (see above) then much later in mild intraspecific aggression. Occasionally two squid would fight over one fish, but the first firm observations came at the time of sexual maturation when mating was seen. As Hurley (1977) noted, there were no obvious interactions among males to form a dominance hierarchy for mate selection. Mating was initiated by males, and both typical forms of mating were observed: "head-to-head" matings in which spermatophores were stored in the *bursa copulatrix*; and male-underneath matings in which spermatophores were deposited in the mantle near the oviduct (cf., Drew 1911; McGowan 1954; Hurley 1977). Females mated promiscuously as they do in nature, and females were also stimulated visually to lay eggs around artificial facsimiles of egg mops (Fig. 16). Males were not observed to guard or defend egg capsules as described by Hurley (1977), but this may have been because relatively few egg capsules were left in the tank each day.

Reproduction

In L.O. 1980 only the subadult stage was reached in 233 d (Yang et al. 1980b, 1983a). Full sexual maturity was achieved in L.O. 1981 and 1982 and spawning of viable eggs occurred from days 196 to 239 and 175 to 226, respectively (Fig. 13). Relatively few egg capsules were laid per female, and these capsules were generally shorter and contained slightly fewer eggs per capsule than those reported from natural populations, but this was probably due to the smaller size of these spawning females (Hixon 1983).

Laboratory cultured *Loligo opalescens* matured precociously and since they are terminal spawners this prevented attainment of full adult size. In the laboratory, males as small as 71 mm ML had fully formed spermatophores and females became sexually mature beginning at about 60 mm ML (Fig. 15). In nature, the average adult size is 150 mm ML for males and 140 mm ML for females, although size at onset of maturity is variable and can be as low as 72 mm ML for males and 81 mm ML for females (Fields 1965; Hixon 1983). Precocious maturation has also been reported in other squid maintained in the laboratory (cf., Durward et al. 1980; Hanlon et

al. 1983). The stimuli (or stressors) that cause this are unknown.

Van Heukelem (1979) reviewed environmental factors that influence maturation in cephalopods and reported that light, temperature, and nutrition are the key stimuli. In our experiments, light was constant (24 h on), temperature was consistent (ca. 15°C) and food was relatively constant and highly available compared with natural populations. However, all three conditions are different from nature. The most interesting result concerns light, which is thought to have a major effect on maturation through the light-optic gland-gonad pathway (cf., Mangold and Froesch 1977; Wells and Wells 1977). Long daylength of high intensity is thought to delay maturation; in our experiments daylength was 24 h but intensity (ca. 4-17 lux) was low compared with full sunlight. However, we do not know what light intensity subadult *L. opalescens* are subject to in nature. Clearly, long daylength alone does not delay maturation in *L. opalescens*. Future experimentation will be necessary to identify the combinations of environmental factors that affect maturation in the laboratory.

Life Cycle Comparisons: Laboratory vs. Fishery Data

In general, five major rearing attempts have been successful in varying degrees: 1) Hurley (1976), to 100 d; 2) Hanlon et al. (1979), to 79 d; 3) L.O. 1980, to 233 d and subadult stage (Yang et al., 1980b, 1983a); 4) and 5) L.O. 1981 and 1982, to sexual maturity and egg laying within 8 mo (this report). From this it is clear that the life cycle can be <1 yr under laboratory conditions.

Fields (1965) stated, based upon fishery data, that "Almost all females spawn at the age of 3 years...." However, more recent field (cf., Recksiek and Frey 1978) and laboratory studies of *L. opalescens* (above) indicate that life span estimates beyond 2 years are excessive. Furthermore, recent books on cephalopod life cycles (Boyle 1983, in press) indicate that few squid live beyond 2 years.

Growth information on laboratory populations is now quite good. The present data allow an accurate assessment by weight from hatching onwards (Fig. 9) and firmly verify that young squid are capable of dramatically fast, exponential growth when food is not limiting. This indicates that in nature squid are capable of exploiting plankton blooms and other instances of greater food availability; the highest feeding rates we estimated (29%) also confirm field observations that squid will eat large quantities of food when available and when necessary. Field estimates of growth by Fields (1965) and Spratt (1978) are compared with laboratory data in Figure 17. Field's data are very conservative (averaging 4 mm/month) and based only upon monthly modal length-frequency diagrams from squid on or near spawning grounds. Spratt (1978) estimated growth from statolith rings and hypothesized that growth is rapid during the first few months then decreases with age. Laboratory growth was much faster, but animals were not subject to environmental fluctuations. We estimate that growth in nature approximates something between the laboratory data and Spratt's data, and that date of hatching, seasonal temperature fluctuations, and food availability result in life cycle variations between 1 and 2 years. One would expect to observe exponential growth of young squid during spring and summer when temperatures and food availability are high, slower logarithmic growth in fall and winter, and spawning the following spring.

Field evidence (McGowan 1954; Fields 1965) and reproductive physiology studies (Grieb and Beeman 1978; Knipe and Beeman 1978) indicate that *L. opalescens* is a terminal spawner (Hixon 1983), and our laboratory observations verify this since all animals died shortly after spawning (Fig. 13).

Rings in statoliths may eventually be used as a reliable age marker to determine growth rate and life span. Our preliminary results in this paper from 43 statoliths of known age support Spratt's (1978) conclusion that ring deposition occurs roughly on a daily basis during the first 65 d. However, our laboratory data indicate that the relationship does not hold well beyond that age, although Spratt suggested that daily ring deposition occurs up to 150 d. Thereafter, Spratt (1978) hypothesized lunar (monthly) rings on statoliths but there are no laboratory data for comparison. Daily, fortnightly, or monthly growth rings have been hypothesized in the squid *Gonatus fabricii* (Kristensen 1980), *Todarodes sagittatus* (Rosenberg et al. 1981), *Illex illecebrosus* (Hurley and Beck 1980), and *Loligo forbesi* (Martins 1982), but there are no hard data to confirm these estimates. The mechanism of ring formation is unclear but may be related to feeding, since in this part of our laboratory study the squid received food during 12 h and none for the next 12, while concurrently there was constant light and no temperature fluctuation (Hixon and Villoch 1984). Hurley et al. (1985) and Dawe et al. (1985) found evidence of daily rings in statoliths by inoculating squid with tetracycline or strontium. Further work is required to

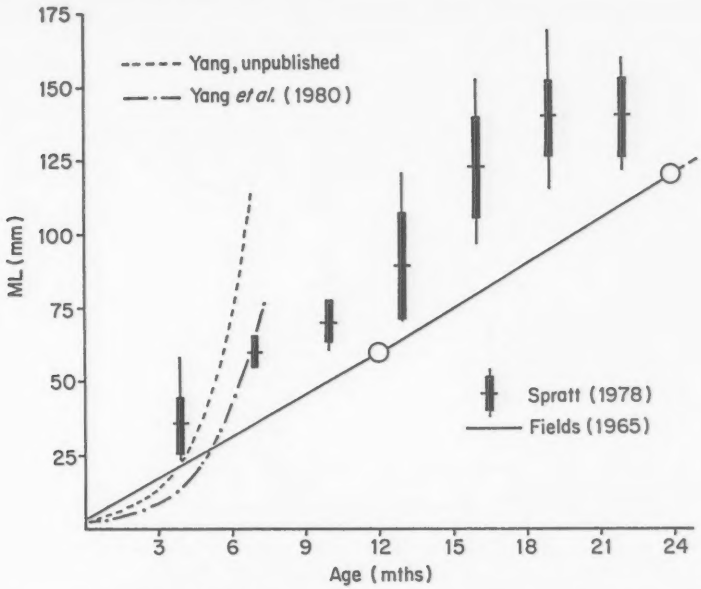


FIGURE 17.—From estimates of growth rate in mantle length of *Loligo opalescens*. Fields (1965) used population data. Spratt (1978) combined age (statolith ring counts) and ML data and calculated a mean (horizontal line), range (vertical line) and standard deviation (vertical bar) values for 3-month intervals throughout the life cycle. Yang et al. data are from laboratory rearing studies (1980b, 1983a, this report) (modified from figure 7.1, Hixon 1983).

determine if and how statolith rings are correlated with age.

A major gap in fisheries studies concerns where the hatchlings go from the spawning grounds. Very few young squid have been captured (Okutani and McGowan 1969; Recksiek and Kashiwada 1979) even in the vicinity of spawning grounds. Hatchlings are positively phototaxic and this may serve to disperse them immediately from the spawning grounds. Thereafter their movements are unknown, although rarely young squid 3.5 to 7.0 mm ML have been caught in neritic plankton samples, usually at depths of 25 to 40 m nearshore in water between 12.5° and 21.0°C (Okutani and McGowan 1969). Detailed knowledge of water currents between spawning grounds and nearshore, combined with monitoring of plankton abundance (especially copepods and larval fish) by surface, bottom and oblique tows may provide important clues about movements and feeding patterns of young-of-the-year squid. Laboratory studies indicate that squid can swim well enough to hold their position against a current by 10 mm ML, or about 40 to 45 d posthatching. By 15 mm ML (ca. 60-80 d) they can form and maintain well-formed schools. The functions of schooling in nature probably relate to defense, feeding and migratory behavior.

The California squid fishery has nearly collapsed since El Niño of 1983, and the squid population has been generally displaced northward as far as southern Canada. Some small spawning populations are still present in southern and central California. It may be rewarding to investigate feeding and migratory patterns of young and adult squid to better understand population recruitment into this ecologically and economically important fishery resource.

Biomedical Research Applications

Loligo opalescens has proved to be a suitable model for giant axon preparations (e.g., Llano and Bezanilla 1980). However, for most axon experiments the largest axons (>400 μm diameter) are needed; this requires the largest squid taken in the fishery, usually 150 mm ML and larger. Our largest squid, 116 mm ML, had an axon about 240 μm in

diameter. Unknown factors in our laboratory environment resulted in precocious sexual maturation and thus smaller animals. Therefore, we are now evaluating the culture potential of *Loligo forbesi*, a much larger squid from the eastern Atlantic, since precocious maturation in that species would still result in axons >500 μm. Preliminary experiments bear out this proposition as we have recently cultured *L. forbesi* to 140 mm ML and 400 μm diameter axons. However, *L. opalescens* would be an excellent model for the giant synapse preparation in which smaller squid are most suitable. Therefore, *L. opalescens*, with a now substantial amount of culture information, may be a highly suitable species in the United States for providing squid on a consistent basis for neuroscience research. Moreover, the recent disappearance of *L. opalescens* (1983-85) from traditional fishing grounds in California make laboratory culture an attractive alternative for animal supply.

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Note: We dedicate this paper to our coauthor and dear friend Dr. Raymond F. Hixon, who passed away on 19 March 1984 as he valiantly fought to recover from chronic myelogenous leukemia.

LITERATURE CITED

ARNOLD, J. M.
1965. Normal embryonic stages of the squid, *Loligo pealei* (Lesueur). Biol. Bull. (Woods Hole) 128:24-32.

ARNOLD, J. M., W. C. SUMMERS, D. L. GILBERT, R. S. MANALIS, N. W. DAW, AND R. J. LASEK.
1974. A guide to laboratory use of the squid *Loligo pealei*. Marine Biological Laboratory, Woods Hole, MA, 75 p.

ATZ, J. W.
1964. Some principles and practices of water management for marine aquariums. *In* J. R. Clark and R. L. Clark (editors), Sea-water systems for experimental aquariums, p. 3-16. U.S. Fish Wildl. Serv., Res. Rep. 63.

BOLETZKY, S. V.
1975. A contribution to the study of yolk absorption in the Cephalopoda. Z. Morphol. Tiere 80:229-246.

BOWER, C. E., D. T. TURNER, AND S. SPOTTE.
1981. pH maintenance in closed seawater culture systems: limitations of calcareous filtrants. Aquaculture 23:211-217.

BOYLE, P. R. (editor).
1983. Cephalopod life cycles, Vol. I: Species accounts. Acad. Press, Lond., 475 p.
In press. Cephalopod life cycles, Vol. II: Comparative reviews. Acad. Press, Lond.

DAWE, E. G., R. K. O'DOR, P. H. ODENSE, AND G. V. HURLEY.
1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). J. Northwest Atl. Fish. Sci. 6:107-116.

DREW, G. A.
1911. Sexual activities of the squid, *Loligo pealei* (Les.). J. Morphol. Wistar Inst. Ana. Biol. Phila. 22(2):327-359.

DUBAS, F., R. T. HANLON, G. P. FERGUSON, AND H. M. PINSKER.
1986. Localization and stimulation of chromatophore motoneurons in the brain of the squid *Lolliguncula brevis*. J. Exp. Biol. 121:1-25.

DURWARD, R. D., E. VESSEY, R. K. O'DOR, AND T. AMARATUNGA.
1980. Reproduction in the squid, *Illex illecebrosus*: first observations in captivity and implications for the life cycle. ICNAF, Sel. Pap. 6, p. 7-13.

FIELDS, W. G.
1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish Bull. 131, 108 p.

FORSYTHE, J. W., AND W. F. VAN HEUKELEM.
In press. Cephalopod growth. *In* P. R. Boyle (editor), Cephalopod life cycles, Vol. II: Comparative reviews. Acad. Press, Lond.

GRIEB, T. M., AND R. D. BEEMAN.
1978. A study of spermatogenesis in the spawning population of the squid, *Loligo opalescens*. *In* C. W. Recksiek and H. W. Frey (editors), Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry, p. 11-21. Calif. Dep. Fish Game, Fish. Bull. 169.

HAMABE, M.
1960. Observations of early development of a squid, *Loligo bleekeri* Keferstein. [In Jpn. with Engl. abstr.] Ann. Rep. Jpn. Sea Reg. Fish. Res. Lab. 6:149-155.

HANLON, R. T.
1978. The biology of the squid *Loligo* (*Doryteuthis*) *plei* in captivity. Ph.D. Thesis, Univ. Miami, Coral Gables, 120 p.
1982. The functional organization of chromatophores and iridescent cells in the body patterning of *Loligo plei* (Cephalopoda: Myopsida). Malacologia 23:89-119.

HANLON, R. T., AND R. F. HIXON.
1983. Laboratory maintenance and culture of octopuses and loliginid squids. *In* C. J. Berg, Jr. (editor), Culture of marine invertebrates: Selected readings, p. 44-61. Hutchinson Ross Publishing Co., Stroudsburg, PA, 386 p.

HANLON, R. T., R. F. HIXON, AND W. H. HULET.
1978. Laboratory maintenance of wild-caught loliginid squids. *In* N. Balch, T. Amaratunga, and R. K. O'Dor (editors), Fisheries and marine service technical report 833, p. 20.1-20.14. Dalhousie University, Halifax, Nova Scotia.
1983. Survival, growth, and behavior of the loliginid squids

Loligo plei, *Loligo pealei*, and *Lolliguncula brevis* (Mollusca: Cephalopoda) in closed sea water systems. Biol. Bull. (Woods Hole) 165:637-685.

HANLON, R. T., R. F. HIXON, W. H. HULET, AND W. T. YANG.
1979. Rearing experiments on the California market squid *Loligo opalescens* Berry, 1911. Veliger 21:428-431.

HIRAYAMA, K.
1966. Influence of nitrate accumulated in culturing water on *Octopus vulgaris*. [In Jpn. with Engl. abstr.] Bull. Jpn. Soc. Sci. Fish. 32(2):105-111.

HIRTLE, R. W. M., M. E. DEMONT, AND R. K. O'DOR.
1981. Feeding, growth, and metabolic rates in captive short-finned squid, *Illex illecebrosus*, in relation to the natural population. J. Shellfish Res. 1:187-192.

HIXON, R. F.
1980a. Growth, reproductive biology, distribution and abundance of three species of loliginid squids (Myopsida, Cephalopoda) in the northwest Gulf of Mexico. Ph.D. Thesis, Miami, Coral Gables, 233 p.
1980b. Potential commercial squid resources of the Gulf of Mexico - an updated review. Sea Grant Rep. MASGP-80-012 (Mississippi-Alabama Sea Grant Consortium), p. 54-73.
1983. *Loligo opalescens*. *In* P. R. Boyle (editor), Cephalopod life cycles, Vol. I: Species accounts, p. 95-114. Acad. Press, N.Y., 475 p.

HIXON, R. F., R. T. HANLON, S. M. GILLESPIE, AND W. L. GRIFFIN.
1980. Squid fishery in Texas: biological, economic, and market considerations. Mar. Fish. Rev. 42(7-8):44-50.

HIXON, R. T., AND M. R. VILLOCH.
1984. Growth rings in the statoliths of young laboratory cultured squids (*Loligo opalescens*). Am. Malacol. Bull. 2:93.

HULET, W. H., M. R. VILLOCH, R. F. HIXON, AND R. T. HANLON.
1979. Fin damage in captured and reared squids. Lab. Anim. Sci. 29:528-533.

HURLEY, A. C.
1976. Feeding behavior, food consumption, growth, and respiration of the squid *Loligo opalescens* raised in the laboratory. Fish. Bull., U.S. 74:176-182.
1977. Mating behavior of the squid *Loligo opalescens*. Mar. Behav. Physiol. 4:195-203.

HURLEY, G. V., AND P. BECK.
1980. The observation of growth rings in statoliths from the Ommastrephid squid, *Illex illecebrosus*. NAFO SCR. Doc. 80/II/1, 17 p.

HURLEY, G. V., P. H. O'DENSE, R. K. O'DOR, AND E. G. DAWE.
1985. Strontium labelling for verifying daily growth increments in the statolith of the short-finned squid (*Illex illecebrosus*). Can. J. Fish. Aquat. Sci. 42:380-383.

KARPOV, K. A., AND G. M. CAILLIET.
1978. Feeding dynamics of *Loligo opalescens*. *In* C. W. Recksiek and H. W. Frey (editors), Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry, p. 45-65. Calif. Dep. Fish Game, Fish. Bull. 169.

KNIPE, J. H., AND R. D. BEEMAN.
1978. Histological observations on oogenesis in *Loligo opalescens*. *In* C. W. Recksiek and H. W. Frey (editors), Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry, p. 23-33. Calif. Dep. Fish Game, Fish. Bull. 169.

KRISTENSEN, T. K.
1980. Periodical growth rings in cephalopod statoliths. Dana 1:39-51.

LA ROE, E. T.
1971. The culture and maintenance of the loliginid squids *Sepioteuthis sepioidea* and *Doryteuthis plei*. Mar. Biol. (Berl.) 9:9-25.

LLANO, I., AND F. BEZANILLA.
1980. Current recorded from a cut-open giant axon under voltage clamp. Proc. Natl. Acad. Sci. USA 77(12):7484-7486.

LOUKASHKIN, A. S.
1977. On biology of the market squid, *Loligo opalescens*, a contribution toward the knowledge of its food habits and feeding behavior. Calif. Coop. Ocean. Fish. Invest. Rep. 18:108-111.

MACY, W. K., III.
1980. The ecology of the common squid, *Loligo pealei* LeSueur, 1821, in Rhode Island waters. Ph.D. Thesis, Univ. Rhode Island, Kingston, 249 p.
1982. Development and application of an objective method for classifying long-finned squid, *Loligo pealei*, into sexual maturity stages. Fish. Bull., U.S. 80:449-459.

MANGOLD, K., AND D. FROESCH.
1977. A reconsideration of factors associated with sexual maturation. Symp. Zool. Soc., Lond. 38:541-555.

MARTINS, H. R.
1982. Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. J. Mar. Biol. Assoc. U.K. 62:799-808.

MCCONATHY, D. A., R. T. HANLON, AND R. F. HIXON.
1980. Chromatophore arrangements of hatchling loliginid squids (Cephalopoda, Myopsida). Malacologia 19:279-288.

MCGOWAN, J. A.
1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif. Fish Game 40:47-54.

MOE, JR., M. A.
1982. The marine aquarium handbook: beginner to breeder. Norns Publishing Co., Marathon, FL, 169 p.

O'DOR, R. K., AND M. J. WELLS.
In press. Energy and nutrient flow in cephalopods. *In* P. R. Boyle (editor), Cephalopod life cycles, Vol. II: Comparative reviews. Acad. Press, Lond.

OKUTANI, T., AND J. A. MCGOWAN.
1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California current April, 1954 - March, 1957. Bull. Scripps Inst. Oceanogr. 14, Univ. Calif. Press, Berkeley, 89 p.

RATHJEN, W. F., R. F. HIXON, AND R. T. HANLON.
1979. Squid fishery resources and development in the Northwest Atlantic and Gulf of Mexico. Gulf Caribb. Fish. Inst. 31:145-157.

RECKSIEK, C. W., AND H. W. FREY (editors).
1978. Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish. Bull. 169, 185 p.

RECKSIEK, C. W., AND J. KASHIWADA.
1979. Distribution of larval squid, *Loligo opalescens*, in various nearshore locations. Calif. Coop. Ocean. Fish. Invest. Rep. 20:31-34.

ROPER, C. F. E., C. C. LU, AND F. G. HOCHBERG (editors).
1983. The biology and resource potential of cephalopods. Memoirs of the National Museum of Victoria, Melbourne, Australia, No. 44, 311 p. Brown-Prior-Anderson Pty. Ltd., Burnwood, Victoria.

ROSENBERG, A. A., K. F. WIBORG, AND I. M. BECH.
1981. Growth of *Todarodes sagittatus* (Lamarck) (Cephalopoda, Ommastrephidae) from the Northeast Atlantic, based on counts of statolith growth rings. Sarsia 66(1):53-57.

SOICHI, M.
1976. On the growth and food quantity of young common

squid, *Todarodes pacificus*, in captivity. [In Jpn.] Dosuishi 13(4):79-82.

SPOTTE, S.
1979a. Fish and invertebrate culture. Water management in closed systems. 2d ed. Wiley-Interscience, N.Y., 179 p.
1979b. Seawater aquariums: The captive environment. John Wiley and Sons, N.Y., 413 p.

SPRATT, J. D.
1978. Age and growth of the market squid, *Loligo opalescens* Berry, in Monterey Bay. *In* C. W. Recksiek and H. W. Frey (editors), Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens*, Berry, p. 35-44. Calif. Dep. Fish Game, Fish. Bull. 169.

STRICKLAND, J. D. H., AND R. T. PARSONS.
1972. A practical handbook of seawater analysis. 2d ed. Fish. Res. Board Can., Bull. 167, 310 p.

TAKEUCHI, T.
1969. Strange spawning of the YARI-IKA (*Doryteuthis bleekeri*): letting incubate the eggs by a crab. [In Jpn.] Fish Mag. 1969:86-89.
1976. Spawning behavior of YARI-IKA (*Doryteuthis bleekeri*). [In Jpn.] Fish Mag. 1976:1-4.

VAN HEUKELEM, W. F.
1979. Environmental control of reproduction and life span in *Octopus*: an hypothesis. *In* S. E. Stancyk (editor), Reproductive ecology of marine invertebrates, p. 123-133. The Belle W. Baruch Library in Marine Science, No. 9, Univ. So. Carolina Press, Columbia.

WELLS, M. J., AND J. WELLS.
1977. Cephalopoda: Octopoda. *In* A. C. Giese and J. S. Pearse (editors), Reproduction of marine invertebrates 4, p. 291-336. Acad. Press, Lond.

YANG, W. T., R. T. HANLON, R. F. HIXON, AND W. H. HULET.
1980a. First success in rearing hatchlings of the squid *Loligo pealei* Lesueur 1821. Malacol. Rev. 13:79-80.

YANG, W. T., R. T. HANLON, M. E. KREJCI, R. F. HIXON, AND W. H. HULET.
1980b. Culture of California market squid from hatching - first rearing of *Loligo* to sub-adult stage. [In Jpn. with Engl. abstr.] Aquabiology 2:412-418.
1983a. Laboratory rearing of *Loligo opalescens*, the market squid of California. Aquaculture 31:77-88.

YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, R. T. HANLON, AND W. H. HULET.
1983b. Culture of California market squid from hatching - completion of the rearing cycle to second generation hatchlings. [In Jpn. with Engl. abstr.] Aquabiology 5:328-339.

FISH ASSEMBLAGES IN *MACROCYSTIS* AND *NEREOCYSTIS* KELP FORESTS OFF CENTRAL CALIFORNIA

JAMES LEE BODKIN[1]

ABSTRACT

The abundance and species composition of conspicuous fishes were compared within two canopy forming kelp forests (giant kelp, *Macrocystis pyrifera*, and bull kelp, *Nereocystis luetkeana*) in Central California. The primary investigative method was a subtidal belt transect, in which visual observation was used. The species composition of fish assemblages in the two canopy types was similar. Densities of fish were generally greater in *Macrocystis* than in *Nereocystis* forests. The major difference was the density of midwater species of the genus *Sebastes*. The blue rockfish, *Sebastes mystinus*, was the numerically dominant species in both canopy types. Estimates of the biomass of fish were about 2.4 times greater in *Macrocystis* beds than in *Nereocystis* beds.

Many species of fish exhibit an affinity for substrate and cover within their habitat, such as rock or coral reefs or kelp beds, as well as man-made objects such as piers, jetties, and offshore oil platforms. This structure may provide shelter, a base for foraging activity, or nursery habitat for young fish. Within the temperate nearshore marine environment, macroalgae may provide a large portion of this substrate and cover. Kelp forests are one of the major features of the nearshore environment along the west coast of North America. The two most conspicuous canopy-forming kelps are the giant kelp, *Macrocystis pyrifera*, a perennial, and the bull kelp, *Nereocystis luetkeana*, an annual (Abbott and Hollenberg 1976). Besides the difference in perennial versus annual growth pattern, *Macrocystis* and *Nereocystis* differ markedly in physical structure (Fig. 1) and seasonal patterns of abundance. *Macrocystis* plants typically have many stipes originating from a single large holdfast, and large fronds attached to each stipe throughout its length. *Nereocystis* plants consist of a single stipe, with large fronds only at the distal end. During periods of full development (typically late summer), *Macrocystis* can develop a completely closed canopy, whereas *Nereocystis* typically has a broken canopy. Winter storms usually remove large portions of the *Macrocystis* canopy, but many plants remain secured to the substrate and provide structure within the water column to varying depths throughout the year. *Nereocystis* canopies are also typically removed during these storms, and, because *Nereocystis* is an annual, it provides little or no structure from midwinter through late spring.

Nereocystis may be more abundant than *Macrocystis* in the presence of severe and persistent disturbances such as continued exposure to large swells or heavy grazing pressure (Dayton et al. 1980). In the absence of this pressure, *Macrocystis* may be competitively dominant, in that it forms a dense and often complete surface canopy earlier in the year, and thus may exclude or limit *Nereocystis* which has light-sensitive germination requirements (Dayton et al. 1980, 1984).

This study was designed to test the hypothesis that the fish component of the *Macrocystis pyrifera* community differs from that of the *Nereocystis luetkeana* community in Central California.

METHODS

Studies were conducted from 6 km south to 15 km north of Point Piedras Blancas, San Luis Obispo County, CA (lat. 35°40′N, long. 121°17′W) (Fig. 2). Additional studies were also done near Big Creek, Monterey County, CA (lat. 36°04′N, long. 121°36′W). The surface canopies of kelp beds consist almost exclusively of *Nereocystis* from Point Piedras Blancas north to Ragged Point, an area about 13 km long, but are dominated by *Macrocystis* south of Piedras Blancas. I searched 74 transects in the Piedras Blancas study area and 4 in the Big Creek area: 26 transects in *Macrocystis* forests and 14 in *Nereocystis* in 1982 and 17 in *Macrocystis* and 21 in *Nereocystis* in 1983. Field studies extended from June

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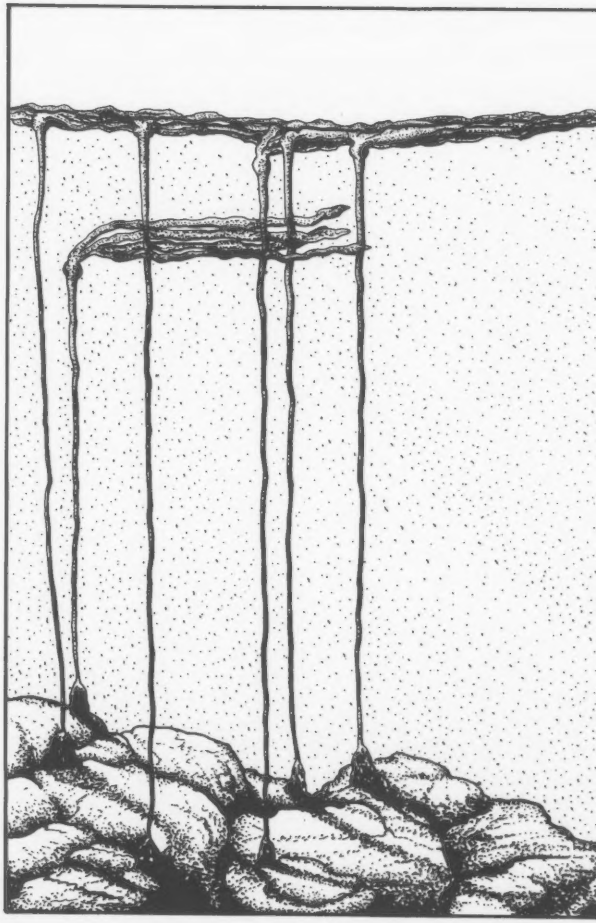

FIGURE 1.—A comparison of the physical structure of *Nereocyst*

reocystis luetkeana (left) and *Macrocystis pyrifera* (right) kelp forests.

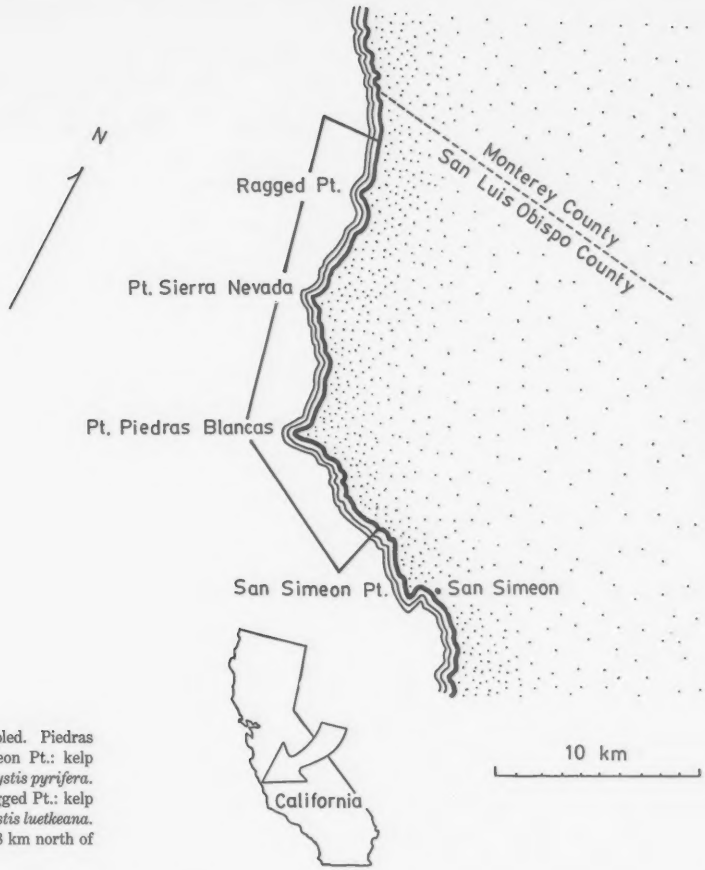

FIGURE 2.—Location of areas sampled. Piedras Blancas Pt., south, to San Simeon Pt.: kelp canopies are dominated by *Macrocystis pyrifera*. Piedras Blancas Pt. north, to Ragged Pt.: kelp canopies are dominated by *Nereocystis luetkeana*. Big Creek (not shown) is about 38 km north of Ragged Pt.

1982 to October 1983. Transects were apportioned evenly throughout early summer to late fall in each of the forest types.

A belt transect, as described by Brock (1954) and modified by Quast (1968), was used with the aid of scuba to conduct subtidal fish surveys. Each survey consisted of two components, benthic and midwater. A 50 m fiberglass tape was extended across the ocean floor in differing compass courses, extending from eye bolts permanently embedded in the substrate, or from the anchor of a dive boat on haphazardly located transect sites. The width of the midwater transect was determined by measuring the horizontal water visibility 2 m above the substrate. This was done by sighting down the transect line (fiberglass tape) toward the zero end, where a small bicolored float (13.5 × 5.5 cm) was suspended 2 m off the bottom. The observer moved away from the float along the line. When the float could not be readily discerned, the position on the tape was recorded. This value was doubled (to include observations on either side of the transect line) to obtain the width of the midwater transect. This survey technique may lead to a slight underestimation of fish densities due to decreasing searching efficiency with increasing distances from observer to observed (Caughley 1977). Surveys were conducted only when visibility exceeded 4.4 m. Horizontal water visibility ranged from 4.4 to 12.1 m (*Macrocystis* $\bar{x}$ = 6.6 m, SE = 2.6; *Nereocystis* $\bar{x}$ = 7.4 m, SE = 0.49). The width of the benthic survey was 4 m (2 m on each side of the transect tape). All sampling

was conducted beneath and within either of the two forest types, in water 6 to 22 m deep. Underwater observations were recorded on formated data sheets using plastic paper.

In conducting the benthic survey, I slowly swam from one end of the transect to the other and identified and enumerated the fish that were observed. A fish was included in the benthic survey if it was observed within 0.5 m of the bottom and was not a member of a school of typically midwater fish located momentarily near the bottom. A fish observed swimming through the transect in front of the diver was included. An effort was made to inspect all crevices, caves, and ledges, and to move aside algae to locate fish. A description of unfamiliar fish was made in the field and its identity later determined in field guides if possible. Small, relatively cryptic species were probably underestimated in the process of these visual surveys (Brock 1982).

The midwater transect was searched about 3 m above the tape. Repetitive ascents and descents were made at 5 m intervals to detect fish occurring throughout the water column. The sizes of very large schools were estimated. All fish observed within the length of the 50 m tape were recorded. Unidentified species were treated as they were during the benthic survey.

After the survey was completed, an index of the bottom profile was recorded by measuring the water depth at each meter mark along the tape. Two methods of determining bottom profile were used: first, an objective, and later, a subjective measure. The objective relief index was the sum of the differences between each of the 50 consecutive depth measurements along the 50 m transect. During the second half of this study (1983) a subjective relief index was assigned to the general vicinity of each transect; this was determined by the greatest vertical relief observed along the transect line: 0 = flat, no relief; 1 = low relief <1 m); 2 = moderate relief (1 to 2 m); 3 = high relief (2 to 4 m); and 4 = extreme relief (more than 4 m).

Two measures of species diversity were used to compare the fish assemblages in *Macrocystis* and *Nereocystis* forests: 1) total number of species found on all transects within one canopy type and 2) the Shannon-Weaver index of diversity, H′ (Pielou 1966).

Because of heterogeneity between sample variances, fish density distributions were compared with the nonparametric Mann-Whitney test. A minimum acceptable level of significance of 0.05 was assigned.

RESULTS

Twenty-seven species of fish were identified within the spatial limits of the transects (Tables 1, 2, 3). An additional 8 species were identified within the kelp forest, but outside the transect limits. Juvenile rockfish were considered a single group, and occasionally an unidentified fish was observed.

In *Macrocystis* forests, 26 species were identified within the transects and 10 species outside the transects; in *Nereocystis* forests, the respective totals were 23 and 4 species. Three additional types of fish were observed that could be identified only to the family level (Table 3). Four species observed only in *Macrocystis* forests were white seaperch, *Phanerodon furcatus*; rainbow seaperch, *Hypsurus caryi*; China rockfish, *Sebastes nebulosus*; and blackeye goby, *Coryphopterus nicholsi*. One species was observed only in *Nereocystis* beds, the jacksmelt, *Atherinopsis californiensis*. Species not observed within both transect types were relatively uncommon, but were observed in and around both forest types during this study.

Fishes that could not be identified to species or family level were rare, occurring on only 6 (8%) of the transects (Table 3).

TABLE 1.—Summary of presence/absence of fish species encountered [midwater (M) and benthic (B), years pooled] throughout study.

Species	*Macrocystis*	*Nereocystis*	Principal habitat
Sebastes mystinus	X	X	M
Sebastes serranoides	X	X	M
Sebastes atrovirens	X	X	M
Sebastes melanops	X	X	M
Sebastes chrysomelas	X	X	B
Sebastes carnatus	X	X	B
Sebastes miniatus	X	X	B
Sebastes rastrelliger	X	X	B
Sebastes caurinus	X	X	B
Sebastes nebulosus	X		B
Sebastes sp. (juveniles)	X	X	M/B
Oxyjulis californica	X	X	M
Aulorhynchus flavidus	X	X	M
Atherinopsis californiensis		X	M
Phanerodon furcatus	X		M
Oxylebius pictus	X	X	B
Hexagrammos decagrammus	X	X	B
Embiotoca lateralis	X	X	B
Embiotoca jacksoni	X	X	B
Orthonopias triacis	X	X	B
Scorpaenichthys marmoratus	X	X	B
Ophiodon elongatus	X	X	B
Rhachochilus vacca	X	X	B
Coryphopterus nicholsi	X		B
Anarrhichthys ocellatus	X	X	B
Jordania zonope	X	X	B
Hypsurus caryi	X		B

Midwater Transects

Differences in abundance of fish in the *Macrocystis* and *Nereocystis* forests were most apparent among the midwater species, primarily within the genus *Sebastes*. Of the nine species of midwater fish (juvenile *Sebastes* treated as a single "species"), three were significantly more abundant in *Macrocystis* than in *Nereocystis* forests: blue rockfish, *S. mystinus*; kelp rockfish, *S. atrovirens*; and olive rockfish, *S. serranoides* (Tables 1, 2). A fourth species, the black rockfish, *S. melanops*, was not observed on *Nereocystis* transects, though it was only occasionally seen in *Macrocystis*.

Although there were no general changes in fish abundance between 1982 and 1983 among the midwater species, some individual species differences were noted. Densities of blue rockfish were significantly lower in 1983 than in 1982 (Table 2). During this same period there was an insignificant increase in the density of juvenile rockfish. Densities of the señorita, *Oxyjulis californica*, appeared to increase within both forest types in 1983, but the increase was significant only when canopy types were combined for each year. This annual variation should be considered in light of the extremely anomolous El Niño event which occurred during this period (Cane 1983), and may be atypical.

Benthic Transects

Among the 19 principally benthic species found in both the *Macrocystis* and *Nereocystis* benthic transects, three (16%) were significantly more abundant in *Macrocystis* forests: Striped seaperch, *Embiotoca lateralis*, painted greenling, *Oxylebius pictus*, and the gopher rockfish, *Sebastes carnatus* (Tables 1, 3). One other species, the kelp rockfish, which occurred on benthic transects, was considered as primarily a midwater species. Gopher rockfish are bathymetrically segregated from the sibling species, *S. chrysomelas* (black-and-yellow rockfish). Gopher rockfish are relatively more abundant at depths >12 to 14 m (Larson 1980). In my study, the densities of black-and-yellow rockfish increased significantly in the second year while during the same period, densities of gopher rockfish decreased.

Due to sampling methodology and the occurrence

TABLE 2.—Mean densities (no. fish/100 m^2) and frequency of occurrence of fishes on midwater transects through kelp (standard error of mean in parenthesis).

Species	Mean densities (fish/100 m^2)						Frequency of occurrence	
	Macrocystis			*Nereocystis*				
	1982	1983	1982-83	1982	1983	1982-83	*Macrocystis*	*Nereocystis*
Sebastes mystinus[1,2] Blue rockfish	19.4	8.25	15.0 (1.8)	6.68	2.09	3.9 (1.0)	1.00	0.82
Sebastes serranoides[1] Olive rockfish	0.51	0.36	0.45 (0.09)	0.17	0.07	0.11 (0.03)	0.74	0.34
Sebastes atrovirens[1] Kelp rockfish	0.19	0.16	0.18 (0.05)	0.007	0.005	0.006 (0.004)	0.44	0.06
Sebastes melanops[1] Black rockfish	0.03	0.01	0.02 (0.009)	0	0	0	0.16	0
Sebastes sp. Juvenile rockfish	3.4	7.7	5.1 (3.1)	0.06	0.95	0.59 (0.5)	0.19	0.11
Oxyjulis californica[2] Señorita	3.1	26.6	12.4 (6.6)	1.6	18.7	11.9 (6.2)	0.40	0.40
Aulorhynchus flavidus Tube-snout			0.43 (0.4)			0.014 (0.01)	0.07	0.06
Atherinopsis californiensis Jacksmelt			0			6.0 (6.5)	0	0.20
Phanerodon furcatus White seaperch			1.37 (1.4)			0	0.05	0
Species observed incidental to transects								
Scomber japonicus Chub mackerel							0	0.09
Myliobatis californica Bat ray							0	0.03
Sphyraena argentea Pacific barracuda							0.02	0
Torpedo californica Pacific electric ray							0.02	0

[1] Difference significant between *Macrocystis* and *Nereocystis*, years combined.
[2] Difference significant between years, kelp canopies combined.

TABLE 3.—Mean densities (no. fish/100 m^2) and frequency of occurrence of fishes on benthic transects through kelp forests (standard error of mean in parenthesis).

Species	Mean densities (fish/100 m^2)						Frequency of occurrence	
	Macrocystis			*Nereocystis*				
	1982	1983	1982-83	1982	1983	1982-83	*Macrocystis*	*Nereocystis*
Sebastes chrysomelas[1] Black-and-yellow rockfish	1.52	1.91	1.67 (0.25)	1.11	2.21	1.77 (0.26)	0.74	0.91
Oxylebius pictus[2,3] Painted greenling	1.13	1.35	1.2 (0.1)	0.21	0.79	0.56 (0.1)	0.86	0.51
Hexagrammos decagrammus Kelp greenling	0.33	0.35	0.34 (0.07)	0.36	0.43	0.40 (0.07)	0.44	0.57
Sebastes carnatus[1,2] Gopher rockfish	1.29	0.76	1.04 (0.2)	0.75	0.22	0.43 (0.15)	0.61	0.31
Embiotoca lateralis[2] Striped seaperch	0.63	1.1	0.84 (0.2)	0.25	0.12	0.17 (0.08)	0.58	0.20
Sebastes atrovirens[2] Kelp rockfish	0.52	0.97	0.70 (0.1)	0.04	0.15	0.11 (0.05)	0.58	0.14
Sebastes sp. Juvenile rockfish	0.87	0.21	0.62 (0.2)	0.23	0.14	0.17 (0.07)	0.42	0.26
Embiotoca jacksoni Black perch	0.39	0.44	0.41 (0.1)	0	0.27	0.16 (0.06)	0.42	0.17
Orthonopias triacis Snubnose sculpin	0.20	0.23	0.21 (0.06)	0.04	0.13	0.09 (0.04)	0.33	0.14
Sebastes mystinus Blue rockfish	0.08	0.26	0.15 (0.05)	0.04	0.17	0.15 (0.05)	0.23	0.17
Scorpaenichthys marmoratus Cabezon			0.107 (0.04)			0.11 (0.04)	0.16	0.20
Ophiodon elongatus Ling cod			0.13 (0.04)			0.09 (0.04)	0.21	0.09
Sebastes melanops[2] Black rockfish			0.209 (0.06)			0.029 (0.02)	0.23	0.06
Rhachochilus vacca Pile perch			0.135 (0.04)			0.0149 (0.01)	0.21	0.06
Sebastes miniatus Vermilion rockfish			0.042 (0.03)			0.094 (0.04)	0.07	0.14
Coryphopterus nicholsi Blackeye goby			0.198 (0.09)			0	0.21	0
Sebastes rastrelliger Grass rockfish			0.0116 (0.01)			0.0143 (0.01)	0.05	0.11
Sebastes caurinus Copper rockfish			0.035 (0.02)			0.0143 (0.01)	0.07	0.03
Anarrhichthys ocellatus Wolf-eel			0.023 (0.02)			0.0143 (0.01)	0.05	0.03
Jordania zonope Longfin sculpin			0.014 (0.01)			0.0143 (0.01)	0.02	0.03
Hypsurus caryi Rainbow seaperch			0.034 (0.01)			0	0.05	0
Sebastes nebulosus China rockfish			0.019 (0.02)			0	0.02	0
Unidentified fish			0.128 (0.09)			0.29 (0.3)	0.05	0.11
Species observed incidental to transects								
Sebastes serriceps Treefish							0.02	0.03
Cephaloscyllium ventriosum Swellshark							0.05	0
Sebastes auriculatus Brown rockfish							0.02	0
Sebastes pinniger Canary rockfish							0.02	0
Clinidae Clinids							0.12	0
Cottidae Sculpins							0.07	0
Gobiesocidae Cling fishes							0.02	0
Unidentified fish							0.12	0.06

[1]Difference significant between years, kelp canopies combined.
[2]Difference significant between *Macrocystis* and *Nereocystis* years combined.
[3]Difference significant between years, *Nereocystis*.

of *Macrocystis* in water up to 4 m deeper than that occupied by *Nereocystis* within the study area, the mean water depth at which surveys were made differed between sites (*Macrocystis* mean depth = 12.2 m; *Nereocystis* mean depth = 10.5 m, $t = 2.73$, $P = 0.008$ (two sample t-test)). When the five transects in *Macrocystis* which occurred at depths beyond the maximum depth of *Nereocystis* transects (16 m) were excluded from analysis, the difference in water depths between sites became insignificant. Following the removal of these deep transects, all species of fish, both midwater and benthic, were reevaluated. There were no changes in the results presented above following this treatment.

There was little correlation between densities of fish and either of the bottom relief indices (r values, 0.025 to 0.482). Throughout the study, bottom relief typically ranged from 1 to 4 m and relief <1 m was not encountered. Mean values of the objective relief index were 44.1 (SE = 2.8) for *Macrocystis* transects and 37.2 (SE = 2.2) for *Nereocystis* transects. This difference resulted in a P value of 0.061 (two sample t-test), which I considered significant. However, when all species of fish which demonstrated significantly different densities between canopy types were reevaluated, after excluding the six *Macrocystis* transects with relief values more than one standard deviation above the mean, no change in results was observed for any species tested.

The total number of species encountered on the transects was 26 in *Macrocystis* and 23 in *Nereocystis*. The two kelp forests had 22 species in common. Five species were found in only one of the two canopy types, although none of these were present in more than 21% of the transects within the canopy in which it was found. The H′ values calculated were 1.76 for *Macrocystis* transects and 1.58 for the *Nereocystis* transects. Although the value of diversity indices has been questioned (Goodman 1975), such indices are widely used in ecological literature. Neither measure of diversity used in the present study indicated differences in the diversity of fish assemblages between the two kelp forest types investigated.

DISCUSSION

Several measures of comparison were considered in the analysis of these two kelp communities: species composition, species diversity, and abundance of fishes. The data presented here demonstrate very little difference in either composition or diversity of fish assemblages (Table 1), while estimates of biomass were markedly higher in giant kelp compared with bull kelp (Table 4).

The single most obvious difference between the two kelp communities was in the abundance of the blue rockfish: mean density of fish (no./100 m^2) was

TABLE 4.—Estimates of biomass of fish of *Macrocystis* and *Nereocystis* kelp forests. Species that were uncommon, (<20% of transects), or small are not included.

Species	*Macrocystis* Density (#/100 m^2)	*Macrocystis* Mean weight[1] (kg)	*Macrocystis* Biomass (kg/100 m^2)	*Nereocystis* Density (#/100 m^2)	*Nereocystis* Mean weight[1] (kg)	*Nereocystis* Biomass (kg/100 m^2)
Midwater transects						
Sebastes mystinus	15.0	0.44	6.6	3.92	0.50	1.96
Sebastes serranoides	0.45	0.63	0.28	0.11	0.72	0.08
Sebastes atrovirens	0.18	0.54	0.09	0.006	0.57	0.003
Sebastes melanops	0.02	0.44	0.009	0	0	0
Oxyjulis californica	12.4	0.024	0.30	11.9	0.024	0.29
Benthic transects						
Sebastes chrysomelas	1.7	0.36	0.61	1.8	0.36	0.65
Sebastes carnatus	1.0	0.36	0.36	0.43	0.36	0.15
Sebastes atrovirens	0.70	0.38	0.27	0.11	0.38	0.04
Sebastes mystinus	0.15	0.44	0.07	0.15	0.50	0.07
Sebastes melanops	0.21	0.44	0.09	0.03	0.44	0.01
Sebastes miniatus	0.04	2.0	0.08	0.09	2.0	0.18
Hexagrammos decagrammus	0.34	0.5	0.17	0.40	0.5	0.2
Embiotoca lateralis	0.84	0.47	0.39	0.17	0.47	0.08
Embiotoca jacksoni	0.41	0.47	0.19	0.16	0.47	0.08
Scorpaenichthys marmoratus	0.11	0.7	0.08	0.11	0.7	0.08
Ophiodon elongatus	0.13	2.6	0.34	0.09	2.6	0.23
Rhachochilus vacca	0.13	0.47	0.06	0.01	0.47	0.005
Total			9.99 kg/100 m^2 = 0.0999 kg/m^2			4.11 kg/100 m^2 = 0.0411 kg/m^2

[1]Mean weights from collections at Piedras Blancas Field Station, U.S. Fish and Wildlife Service, or estimated from mean total lengths.

15.0 in *Macrocystis* and 3.9 in *Nereocystis*. Blue rockfish probably are the largest contributor to the total biomass of kelp forest fish communities in Central California. Miller and Geibel (1973) estimated blue rockfish densities at 6.66 fish/100 m^2 in 1969 and 8.35 in 1970 in *Macrocystis* beds at Hopkins Marine Life Refuge, Monterey County, CA. They suggested that this represents about 50% of the actual biomass because their survey method underrepresented midwater species. Considering this adjustment, my data for blue rockfish in *Macrocystis* forests agree well with theirs. Near Pt. Piedras Blancas, blue rockfish made up 33% and 18% of the mean number of fish within the *Macrocystis* and *Nereocystis* forests, respectively. Assuming an average weight of 440 g (Table 4), blue rockfish contributed about 70% of the total biomass of the *Macrocystis* fish assemblage and about 50% of *Nereocystis* (species weighing a few ounces or less were not included in this analysis). The importance of juvenile blue rockfish as forage for large carnivorous kelp forest fishes (primarily *Sebastes* sp.) has been well documented (Miller and Geibel 1973; Burge and Schultz 1973; Hallacher and Roberts 1985). Tagging studies have suggested that the home range of blue rockfish is relatively small (Miller and Geibel 1973). The evidence given here illustrates the important role that blue rockfish play in the kelp forest communities of central California.

My estimate of the biomass of fish within each of the two canopy types (Table 4) included only species that were relatively common and of sufficient size to contribute significantly to the total. For example, although the estimated mean weight of *Oxyjulis californica* was only 24 g, its abundance made its total contribution rather large.

My data showed that in this study area off Central California *Macrocystis* supported a larger standing crop of fish, primarily midwater species of the genus *Sebastes*, than did forests of *Nereocystis* (Table 4). The following explanations are offered for the observed differences. These explanations are not mutually exclusive; several or all of the proposed explanations may have contributed to the observed patterns.

1) The amount of algae consumed by blue rockfish fluctuates seasonally. Hallacher and Roberts (1985) showed that blue rockfish may use algae as a major source of energy during the non-upwelling period (September through March), which partly coincides with the period of minimum development in *Nereocystis* forests. During this period blue rockfish may rely on *Macrocystis* directly as a food source, or indirectly as a substrate from which invertebrates are taken. The resulting increased biomass of blue rockfish in *Macrocystis* may help support larger numbers of other carnivorous fish. Four of the seven species that were densest in *Macrocystis* (Table 5) forests are known to rely heavily on juvenile rockfish for food (Hallacher and Roberts 1985). Although juvenile rockfish densities were not statistically greater in the *Macrocystis* forest (Table 2) because of large variations in densities (occurring on transects in either very large or very small schools), they were generally more available in *Macrocystis* forests. Subsequent field observations of juvenile rockfish in central California kelp forests have indicated that kelp forest rockfish recruitment may have been poor during the course of this study.

TABLE 5.—Summary of species for which densities in the two kelp types differed significantly.

Species	Canopy type which presented significantly higher density
Midwater	
Sebastes mystinus Blue rockfish	*Macrocystis*
Sebastes serranoides Olive rockfish	*Macrocystis*
Sebastes atrovirens Kelp rockfish	*Macrocystis*
Sebastes melanops Black rockfish	Observed on *Macrocystis* midwater transects only
Benthic	
Sebastes carnatus Gopher rockfish	*Macrocystis*
Embiotoca lateralis Striped seaperch	*Macrocystis*
Oxylebius pictus Painted greenling	*Macrocystis*
Sebastes atrovirens Kelp rockfish	*Macrocystis* (considered primarily as a midwater species)

2) The perennial nature of *Macrocystis* forests compared with the annual nature of *Nereocystis* forests may contribute to increased fish densities in *Macrocystis* forests. *Macrocystis* forests provide some structure throughout the year with new growth providing both vertical and canopy structure 1 to 3 mo earlier than *Nereocystis*. This temporal stability may afford necessary habitat structure within the water column permiting relatively higher densities of fish.

3) Differences in abiotic factors such as the physical orientation of the reef systems to oceanic swells and the resultant surge and scour effects may play a role in determining habitat suitability for some species of fish. The effects of sediment transport and scouring, caused by water movement,

would be most evident at the sea floor and may in fact have contributed to the observed differences in densities in the bottom dwelling surf perch (Table 5). My data indicated that the major differences in densities of fish were in midwater species, suggesting that exposure to bottom disturbance per se was not a primary influence on observed patterns.

4) The differing physical characteristics of the *Macrocystis* and *Nereocystis* plants themselves may play a role in determining their suitability as habitat for kelp bed fishes. During periods of full development, within this study area, *Macrocystis* typically has widely spaced, thick bundles of stipes with large fronds throughout the water column, leading to a canopy that is frequently closed. *Nereocystis*, in contrast, has single, frondless stipes with large terminal fronds that generally form a broken surface canopy (Fig. 1). Due to the distinct physical structure of these two plants, both within the water column and at the canopy, the foliage biomass is usually considerably greater within the *Macrocystis* forest. This abundance of structure, combined with its persistance over time, may enhance the carrying capacity of giant kelp forests compared with those of bull kelp (Leaman 1980).

A comparison of the standing crop estimates presented in this study is made with those from other marine reef systems in Table 6. While values for both *Macrocystis* and *Nereocystis* forests are below those representing fringing coral reefs (Brock 1954; Randall 1963), my estimates for *Macrocystis* forests compare favorably with the upper values obtained in Monterey, CA (Miller and Geibel 1973) and northeast New Zealand (Russell 1977), while the *Nereocystis* estimate corresponds to the estimates from Southern California *Macrocystis* forests (Quast 1968; Larson and DeMartini 1984).

In conclusion, *Macrocystis* forests supported a biomass of fish about 2.4 times greater than that supported by *Nereocystis* forests (Table 4) where perennial, water column foliage provided a more persistant, structurally diverse habitat. Larger numbers of midwater fish, primarily *S. mystinus*, found in the *Macrocystis* forest can account for this difference.

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TABLE 6.—Comparison of biomass estimates of fish from marine communities (after Russell 1977).

Location and reference	Bottom type	Standing crop ($kg.m^2$)
Hawaii (Brock 1954)	Fringing coral reef: open sand, broken rock, coral reef, reef flat	0.001-0.0184
Virgin Islands (Randall 1963)	Fringing coral reef: boulders, coral	0.160
Southern California (Quast 1968)	Kelp bed: broken rocky bottom, dense algal cover	0.035[1]
Southern California (Larson and DeMartini 1984)	Cobble, low relief *Macrocystis* forest	0.039-0.065
	Cobble, low relief kelp-depauperate	0.024
Monterey Bay, CA (Miller and Geibel (1973)	Kelp bed: broken rocky bottom dense algal cover, rocky reef	0.001->0.112
N.E. New Zealand (Russell 1977)	Rocky reef: open low relief, sparse algal cover.	<0.001
	Rocky reef: high bottom relief, extensive algal cover	0.103
Central California (Present study)	Rocky reef: high bottom relief; *Macrocystis* canopy	0.0999
	Nereocystis canopy	0.0411

[1]Average estimate.

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LITERATURE CITED

ABBOTT, I. A., AND G. J. HOLLENBERG.
1976. Marine algae of California. Stanford University Press, Stanford, CA.

BROCK, R. E.
1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32:269-276.

BROCK, V. E.
1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:297-308.

BURGE, R. T., AND S. A. SCHULTZ.
1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

CANE, M. A.
1983. Oceanographic events during El Niño. Science 222: 1189-1195.

CAUGHLEY, G.
1977. Analysis of vertebrate populations. John Wiley and Sons, Lond.

DAYTON, P. K., V. CURRIE, T. GERRODETTE, B. D. KELLER, R. ROSENTHAL, AND D. VEN TRESCA.
1984. Patch dynamics and stability of some California kelp communities. Ecol. Monogr. 54:253-289.

DAYTON, P. K., B. D. KELLER, AND D. A. VEN TRESCA.
1980. Studies of a nearshore community inhabited by sea otters. Final Report MMC-78/14. Mar. Mammal Comm., Wash., D.C., 91 p. (Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., as PB81-109860.)

GOODMAN, D.
1975. The theory of diversity-stability relationships in ecology. Q. Rev. Biol. 50:237-266.

HALLACHER, L. E., AND D. ROBERTS.
1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: Sebastes) of Carmel Bay, California. Environ. Biol. Fish. 12(2):91-110.

LARSON, R. J.
1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50:221-239.

LARSON, R. J., AND E. E. DEMARTINI.
1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. Fish. Bull., U.S. 82:37-53.

LEAMON, B. M.
1980. The ecology of fishes in British Columbia kelp beds. I. Barkley Sound *Nereocystis* beds. Fish. Dev. Rep. 22. Ministry of Environment, British Columbia, 100 p.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rock fish and ling cod life histories; a reef ecology study and a giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

PIELOU, E. C.
1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theoret. Biol. 10:370-383.

QUAST, J. C.
1968. Estimates of the population and standing crop of fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp bed resources in southern California, p. 57-79. Calif. Dep. Fish Game, Fish Bull. 139.

RANDALL, J. E.
1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3:31-47.

RUSSELL, B. C.
1977. Population and standing crop estimates or rocky reef fishes of northeastern New Zealand. N.Z. J. Mar. Freshw. Res. 11:23-36.

LIFE HISTORY AND LARVAL DEVELOPMENT OF THE GIANT KELPFISH, *HETEROSTICHUS ROSTRATUS* GIRARD, 1854

CAROL A. STEPIEN[1]

ABSTRACT

Life history data from about 1,200 giant kelpfish, including age, length, and weight relationships, are described and analyzed. Additionally, differences in habitats and behavior between larvae, juveniles, and adults are reported. Female giant kelpfish were found to be larger than males at given ages past sexual maturity. Age data indicate that females live longer and all individuals larger than 28 cm TL collected in this study were females. Males guard the algal nests until hatching, about 2 weeks after spawning. Giant kelpfish from nests collected in the field were reared in the laboratory, surviving for up to 9 months. Feeding and development of laboratory-reared larvae were compared with field-collected specimens. In situ, they school in the kelp canopy until 2 months old, gradually developing juvenile coloration and becoming increasingly thigmotactic and solitary. Giant kelpfish reach sexual maturity at 1-1.5 years, at which time they commence to defend territories in given plant habitats.

The cryptically colored giant kelpfish, *Heterostichus rostratus*, is abundant in southern California kelp forests and surrounding subtidal plant habitats. *Heterostichus* is one of the largest members of the clinid family, reaching a length of 41.2 cm and an age of 5 yr (J. E. Fitch in Feder et al. 1974). Although ranging from British Columbia, Canada, to Cape San Lucas, Baja California, Mexico, it is most commonly found from Point Conception to central Baja in depths of 35 m (Roedel 1953). Giant kelpfish occur in three different colormorphs—red, brown, and green—which closely match the color of their surrounding plant habitats (Hubbs 1952; Stepien 1985, 1986). They additionally exhibit four different dark melanin patterns, which appear superimposed on the basic color of the fish and, unlike colormorphs, can change rapidly (Stepien 1985, 1986).

Giant kelpfish spawn year-round, but most frequently during spring months (Limbaugh 1955; Feder et al. 1974). The eggs are attached to algal nests with entangling threads that extend from the egg membranes (Holder 1907; Feder et al. 1974). The males alone guard the nests from predators until hatching, averaging 2 wk after spawning (Coyer 1982). Giant kelpfish are relatively well-developed at hatching and are planktonic for several weeks. They school in the kelp canopy until they are about 6 cm long, then develop juvenile coloration and become solitary, living close to nearshore algae (Limbaugh 1955).

Although *Heterostichus* larvae are not uncommon in the nearshore ichthyoplankton, their development has not been previously described. *Heterostichus* egg morphology was described by Barnhart (1932), and the egg-laying process was described by Holder (1907). Matarese et al. (1984) published two drawings of kelpfish larvae. Although diet and some aspects of general life history have been described qualitatively by several investigators (Hubbs 1920, 1952; Roedell 1953; Limbaugh 1955; Quast 1968; Hobson 1971; Feder et al. 1974; Hobson et al. 1981; Coyer 1982) and one quantitative study was conducted on feeding and distribution of juveniles and adults in giant kelp (Coyer 1979), specific morphometric data for larval, juvenile, and adult stages have not previously been reported. This paper presents life history data, including the following: 1) Differences in larval, juvenile, and adult habitats and behavior; 2) size, weight, and age relationships, including differences between males and females; and 3) the sequence of larval development and metamorphosis.

MATERIALS AND METHODS

Collection and In Situ Observations

In situ observations were made during approximately 280 scuba dives from 1978 to 1983, the majority in the vicinity of the University of Southern California's Catalina Marine Science Center

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(CMSC) on Santa Catalina Island (Fig. 1). Most observations and collections were made in protected cove areas having well-developed kelpbeds of the giant kelp, *Macrocystis pyrifera*, and associated plant habitats, including surfgrass, *Phyllospadix torreyi*, and red and brown algae. Approximately 1,200 giant kelpfish were observed during the course of the study. The aging and sexing study material from Catalina was also supplemented by 42 specimens collected from subtidal sites off the southern California mainland, including Ventura, Lunada Bay on the Palos Verdes Peninsula, Huntington Beach, and La Jolla (Fig. 1).

Kelpfish were collected using a 0.5 × 0.8 m net, mounted on a 1 m long handle and constructed of 0.25 cm mesh dyed either brown or red to match the kelpfish algal habitats (it was found that white netting alarmed the fish, making them difficult to

FIGURE 1.—Giant kelpfish collection sites (open triangles) off the southern California coast.

catch). Kelpfish were collected by sliding the net forward and downward over the fish. Collection of kelpfish was facilitated by their habit of hiding in algae when pursued rather than escaping by rapid swimming. Those that were actively swimming (usually through the kelp canopy) were less frequently captured. They were placed in a collecting bucket having mesh sides, a snap-on lid, and a funnel entryway, preventing escapes when the lid was opened for other fish. Care was taken to avoid putting the larger kelpfish in the same bucket as the smaller ones, because the smaller ones were occasionally eaten by the larger ones.

Life History Data From Juveniles and Adults

In the present study, 140 juveniles and adults of representative sizes (ranging from 10 to 42 cm TL) were measured live to the nearest 0.1 cm. Total length (TL) was found to be more quickly measurable than standard length (SL). Both SL and TL were measured, in order to allow comparisons with other studies. Kelpfish were weighed to the nearest 0.1 g on a triple-beam balance while briefly contained in plastic bags, in which they were quiescent and unabraded. These data were graphed, and regression and F-test analyses were performed (Sokal and Rohlf 1981; Zimmerman and Kremer 1983).

The fish were sexed and aged. Females had clear or pink, rounded ovaries and most individuals over 14 cm TL had clearly visible developing eggs. Male gonads were cream-colored and had a characteristic ventral groove. In cases when sex of juveniles was questionable, the gonads were examined under a dissection microscope.

Otoliths (sagitta) were removed and stored dry in labeled glass. They were briefly submerged in water and examined against a black background with a dissecting microscope (25-50× magnification) for ring counting (Fig. 2). Ages were determined by counting alternating white (opaque) and translucent (hyaline) bands, each representing 6 mo of growth,

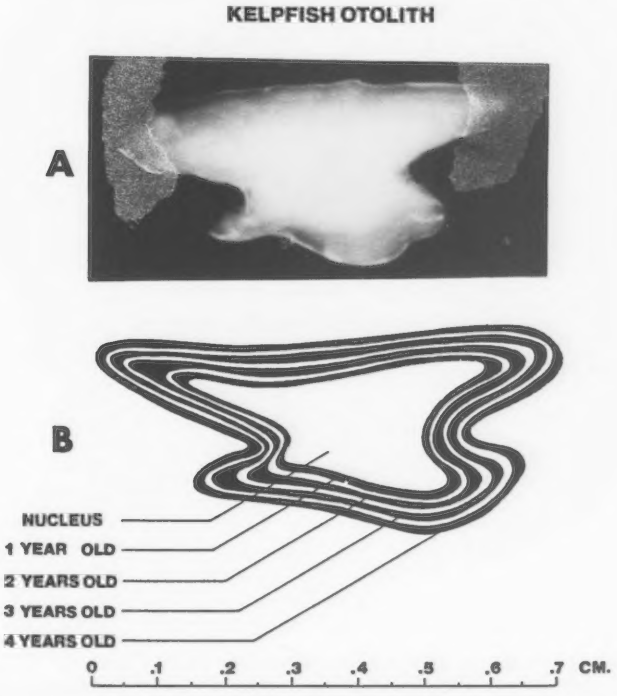

FIGURE 2.—(A) Photograph of otolith (actual length = 6.5 mm) of a 4 yr-old female giant kelpfish, 33 cm TL. (B) Drawing of otolith (sagitta) showing ring counts.

using standard methods outlined by Fitch (1951), Jensen (1965), and Collins and Spratt (1969). Each pair of otoliths was read independently by me and another reader, neither knowing the identity of the fish. Our age estimates were in agreement in 80% of the examinations. When differences in ring count occurred, a joint reevaluation was made.

Total length versus age comparisons were graphed, and regression analysis and *F*-tests were performed on the log-log transformations. Mean sizes of male and female kelpfish in age classes where differences appeared to occur were tested for significance using *t*-tests and 2-way ANOVA. Separate regression equations were also calculated for males and females, and ANCOVA was performed to determine whether the distributions were significantly different (Sokal and Rohlf 1981).

Seasonal population structure was estimated from collection data taken from February 1981 through January 1983. Kelpfish were grouped in six size classes. Distribution of kelpfish in size classes was analyzed for significant seasonal variations using contingency tables and *G*-tests (Sokal and Rohlf 1981).

Larval Rearing

Nine giant kelpfish nests were collected, four in spring 1980 and five in spring 1982, off Santa Catalina Island. Both parents of the eggs were collected in three cases when spawning was observed. In six cases, only the male parents, which were guarding the nests, were collected. Eggs were also laid in the laboratory on five separate occasions, but did not hatch normally, apparently because of inadequate dispersion in the nests.

Algal nests containing eggs were suspended from a glass rod connected to an electric stirring device, simulating wave motion in shallow subtidal habitats (Fig. 3A). This method substantially decreased bacterial and fungal attacks. Parents were not kept with the eggs, as both males and females were sometimes found to eat eggs in the laboratory. Nests were placed in aerated 190 L plastic containers cooled in 1 m deep aquaria of running seawater. Filtered seawater in the containers was replaced every few days. Several eggs were removed daily for examination of development.

Newly hatched larvae were isolated in lightly aerated 76 L brown plastic containers bathed in large aquaria. Kelpfish larvae were fed laboratory-raised *Brachionus plicatilis* (marine rotifers) within 24 h after hatching. *Brachionus plicatilis* were cultured in high densities of the green flagellate, *Tetraselmis tetrahele*, which was grown in a nutrient-rich medium under constant light, following methods developed for feeding northern anchovy larvae (Theilacker and McMaster 1971). *Brachionus plicatilis*, ranging from 0.01 × 0.02 mm to 0.07 × 0.20 mm in size, were maintained in the larval kelpfish containers at concentrations of 10-40/mL. At age 1 wk, kelpfish larvae were changed from closed to open containers of filtered and aerated running seawater, having two 20 × 30 cm panels of 100 μm mesh.

After age 2 wk, kelpfish larvae were also fed wild plankton, which primarily contained various developmental stages of the copepod *Acartia* sp. (92% wet weight) and some barnacle nauplii and cyprid larvae (7% wet weight). Wild plankton were collected using a submersible pump attached to a float off the laboratory pier. A light was suspended over the pump and the system connected to an electrical timer. Plankton were filtered through a 335 μm mesh bag into a 190 L plastic container. The container had a removable inner 100 μm mesh lining and a spillover pipe, retaining only appropriate-sized plankton between the two filter bags (Fig. 4). Best copepod catches were obtained from dusk to 2 h after sunset. Running filtered seawater and an aerator were used to maintain temperature and oxygen levels in the collecting container until the fish larvae were fed the following morning. Densities averaged 1-3/mL, which have been shown to support high survival rates in laboratory rearing of other fish larvae (Houde 1973; Hunter 1981).

When plankton catches were low, giant kelpfish diet was supplemented with cultured *Artemia salina* (brine shrimp) nauplii. *Brachionus plicatilis* were discontinued after age 3 wk and plankton continued until age 3 mo. After age 2 mo, diet was supplemented with frozen adult brine shrimp, Tetramin[2] commercial flake food, and live mysids captured from net tows in kelpbeds.

Ten larvae were removed every 2 d during the first 2 wk of development for measurement and description. After this period, 10 larvae were examined weekly until 2 mo had elapsed. All measurements were made on fresh material. Drawings of several stages of larval development were made using a camera lucida and a dissecting microscope.

Gut contents of three specimens from each weekly sample through age 4 wk were analyzed. While viewing with a dissecting microscope, guts were dissected away from the body and food particles

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

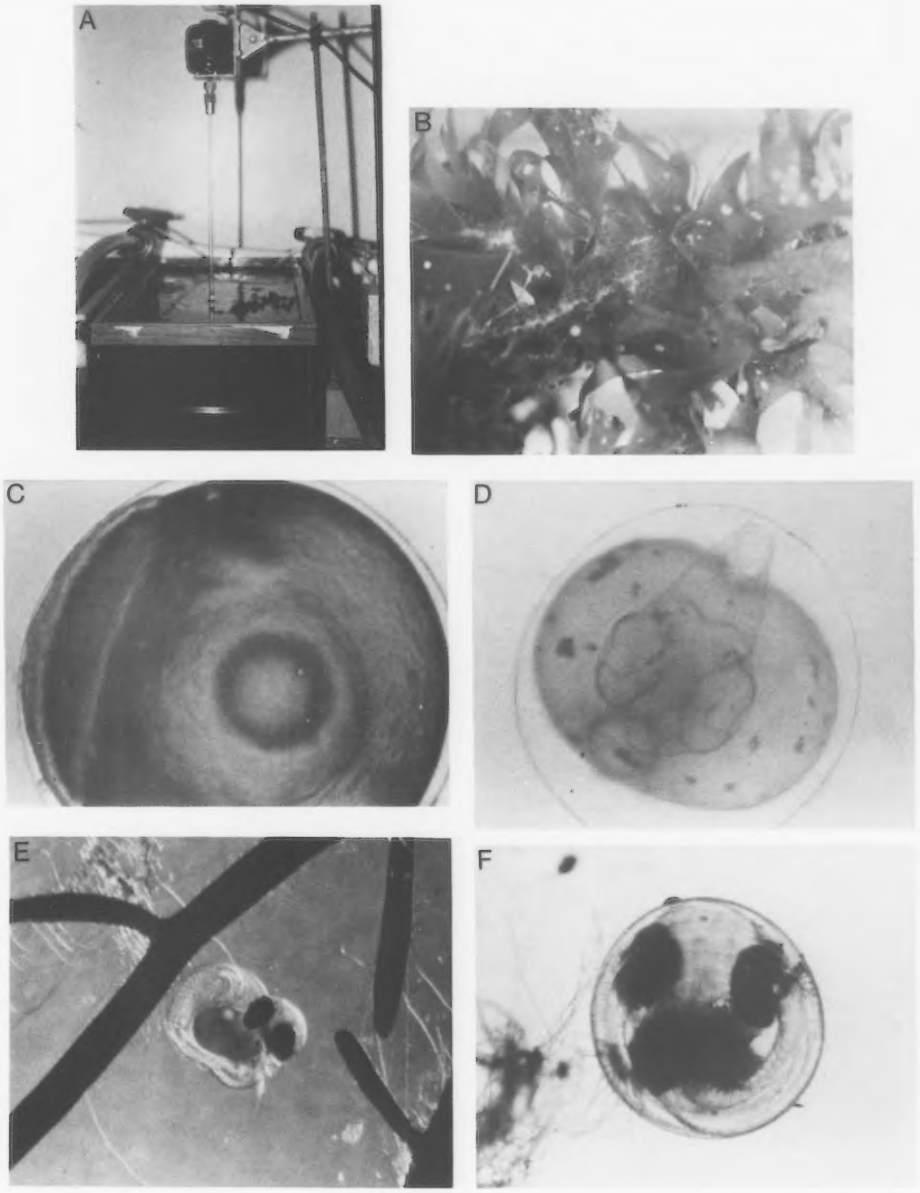

FIGURE 3.—(A) Giant kelpfish nest in aquarium, attached to an electric stirrer, which simulated wave motion. (B) Photograph of nest with eggs in brown algae, taken with 70 mm macrolens. (C) Photograph under compound scope of 24-h kelpfish egg showing blastodisc, egg diameter = 1.4 mm. (D-F) Developing kelpfish eggs photographed under dissection microscope (diameters = 1.4 mm). (D) 72 h after spawning. (E) 10 d after spawning. Note adhesive threads attaching egg to red alga. (F) 12 d after spawning.

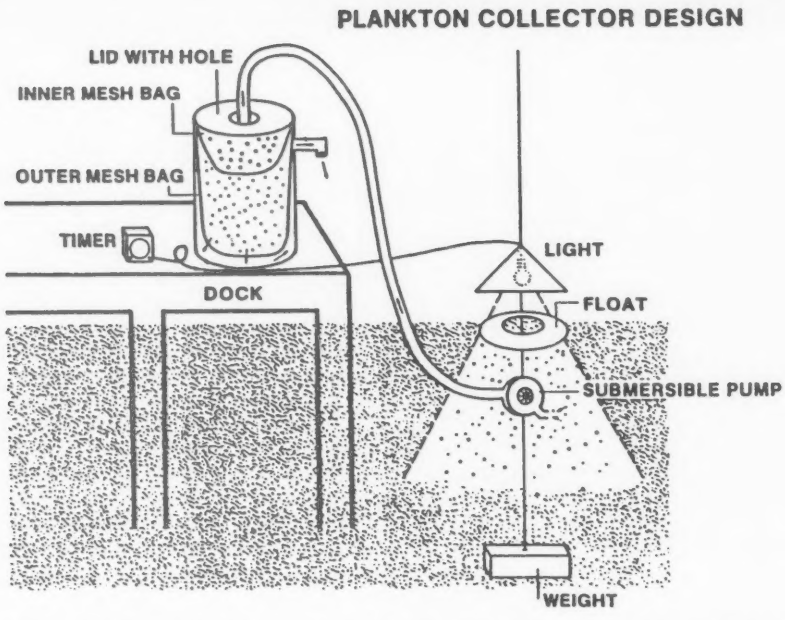

FIGURE 4.—"Automatic" plankton collector design for feeding giant kelpfish larvae. Plankton were attracted to light on timer after dark. Submersible pump, suspended beneath the float, pumped plankton into large plastic container on dock. Plankton ranging from 100 to 325 μm were filtered between two mesh bags. Aeration and running seawater kept the plankton alive.

teased out using either a single human hair or a modified paint brush from which only a few long strands protruded. Gut contents were viewed under a compound microscope and identified, and average lengths and widths of prey items were recorded.

At age 2 mo, the kelpfish larvae were moved to containers having 0.3 cm mesh panels and containing artificial plant habitats (see Stepien 1985 and 1986). They were subsequently measured bimonthly and their development described. Development and feeding of laboratory-reared kelpfish larvae were also compared with 20 field-collected individuals. Kelpfish larvae of various ages and sizes were collected in hand nets while night-lighting from a dock and while scuba diving in kelpbed canopies using a 1 mm mesh handnet. Other kelpfish larvae were examined from bongo net collections made in Santa Monica Bay in 1982. Their development was compared with similar-sized laboratory-reared larvae. Gut contents of four early-stage larvae (estimated 0-9 d old) were analyzed for food types and sizes, in comparison with laboratory-reared kelpfish.

RESULTS

Spawning

Giant kelpfish nests were guarded by the male parent, the eggs being interspersed and held by adhesive threads in either red or brown algae (Fig. 3B). Seven of the nine nests collected were located in isolated clumps of algae, and all were found between 6 and 12 m deep. Kelpfish nests were most common in the red alga *Gelidium nudifrons* (6 of 9 nests collected) in areas where clumps of taller brown algae covered patches of red algae. Three of the nests were located in brown algae, two in *Cystoseira neglecta*, and one in *Sargassum muticum*.

The male parent hid in the overlying clump of brown algae, emerging to chase away intruding fishes. Male kelpfish were observed to defend their nests against other kelpfish, sheephead, and rock wrasse. Female kelpfish may spawn several times a year since a female kept in the laboratory laid eggs twice within 3 mo. Gonads of all females examined after spawning were almost entirely spent. Since

all eggs in the nests examined were in similar stages of development, it is likely that each nest contains the eggs of a single female. After spawning (the behavior sequence of which is described in Coyer 1982), the male kelpfish chases away the female parent, as was observed in the laboratory on three separate occasions. In one case, the male's repeated pursuits resulted in the female jumping out of the aquarium.

Eggs occurred in two different colors, red and brown, which microscopic examination showed was due to color of the yolk. All eggs in a given nest were either red or brown and remained that color throughout development. Nest and egg color did not always match. Brown eggs were found in four nests of red algae and two nests of brown algae, while red eggs were found in two nests of red algae and one nest of brown algae.

Fertilized eggs laid in the laboratory developed poorly and few of them hatched, apparently due to abnormal dispersal in the algal nests by the females. In all three cases of laboratory spawnings, eggs were laid in clumps rather than being well-spaced throughout the algae, as observed in field-collected nests. Freshly laid nests were collected in the field on three occasions from pairs that had just completed spawning. Two of the three spawning females were brown colormorphs and one was a red morph, but all three showed the barred melanin pattern. All nine field-collected male parents were brown colormorphs exhibiting the characteristic male nuptial striped melanin pattern (Coyer 1982; Stepien 1985, 1986).

Egg Development and Hatching

Eggs from freshly laid nests hatched in 12-17 d at 18°C, the largest number hatching in 13 d. Eggs averaged 1.4 mm in diameter and nests contained an average of 700 eggs, ranging from 400 to 1,200 eggs. An estimated 800 of the 1,200 eggs hatched from the most successful laboratory incubation. Nests that were rotated vigorously and kept well-aerated produced the most successful hatchings.

The sequence of egg development is summarized in Table 1 and photographs of the developing eggs are shown in Figure 3. Hatching occurred from day 14 through day 15. Hatching took about 20 min, the larvae emerging head-first from the egg membrane.

Early Larval Development (Prenotochord Flexion)

Giant kelpfish larvae can be distinguished from other southern California clinid larvae by their large numbers of myomeres, averaging 55-59. Newly hatched larvae had large yolk sacs and well-developed mouths, guts, melanophores, and fin folds and averaged 6.2 mm TL (Fig. 5A). Larvae floated upside-down, yolk up, for the first 24-36 h after hatching. They swam with wriggling movements, lasting about 30 s, interspersed with longer periods of inactivity, lasting up to several minutes.

Yolk sacs were present 36-48 h after hatching. Two-day-old larvae averaged 7.0 mm TL and swam strongly upright, showing positive attraction to light and concentrating near the white mesh areas of the containers. After 4 d, the larvae were less positively phototactic, concentrating towards the bottom of the containers. Mean sizes and a summary of the sequence of larval development are listed in Table 2. Illustrations of larvae are found in Figure 5.

Later Larval Development (Postnotochord Flexion)

Flexion of the notochord had begun by 7-9 d and an average size of 8.5 mm (ranging from 7.6 to 8.9 mm, $N = 12$). Field-collected giant kelpfish larvae also showed the beginnings of notochord flexion at a similar size (7.4-9.3 mm, $N = 5$). Size at notochord flexion is smaller than that reported by Matarese et al. (1984) for other clinid larvae.

Two-week-old giant kelpfish larvae began swimming in organized schools, which also were observed in situ in giant kelp canopies. Other researchers have also noted this phenomenon (Feder et al. 1974), which was not observed in giant kelpfish past the age of 2 mo in both the laboratory and the field. By 3 wk, the schooling larvae became progressively more difficult to catch with dip nets, exhibiting well-

TABLE 1.—Summary of kelpfish egg developmental stages.

Time after spawning	Developmental features
24 h	well-developed blastodisc, beginnings of epiboly
36 h	head fold apparent, neural tube forming
72 h	embryo wrapped 180° around egg's circumference; notochord, somites, eyes, and lenses visible
6 d	embryo wrapped 240° around egg's circumference, myomeres well-developed, lenses of eyes pigmented, heart beating 95 times per minute
10 d	yolk shrunk to 1/2 size of egg; embryo curled 1.5 times around egg; mouth differentiated; gut, liver, and inner ear developing
12 d	otoliths and pectoral and dorsal fin folds visible, vigorous tail movements, heart beats 90 to 100 times per minute
14 d	hatching at 18°C., larva exits head-first, hatching takes about 20 min

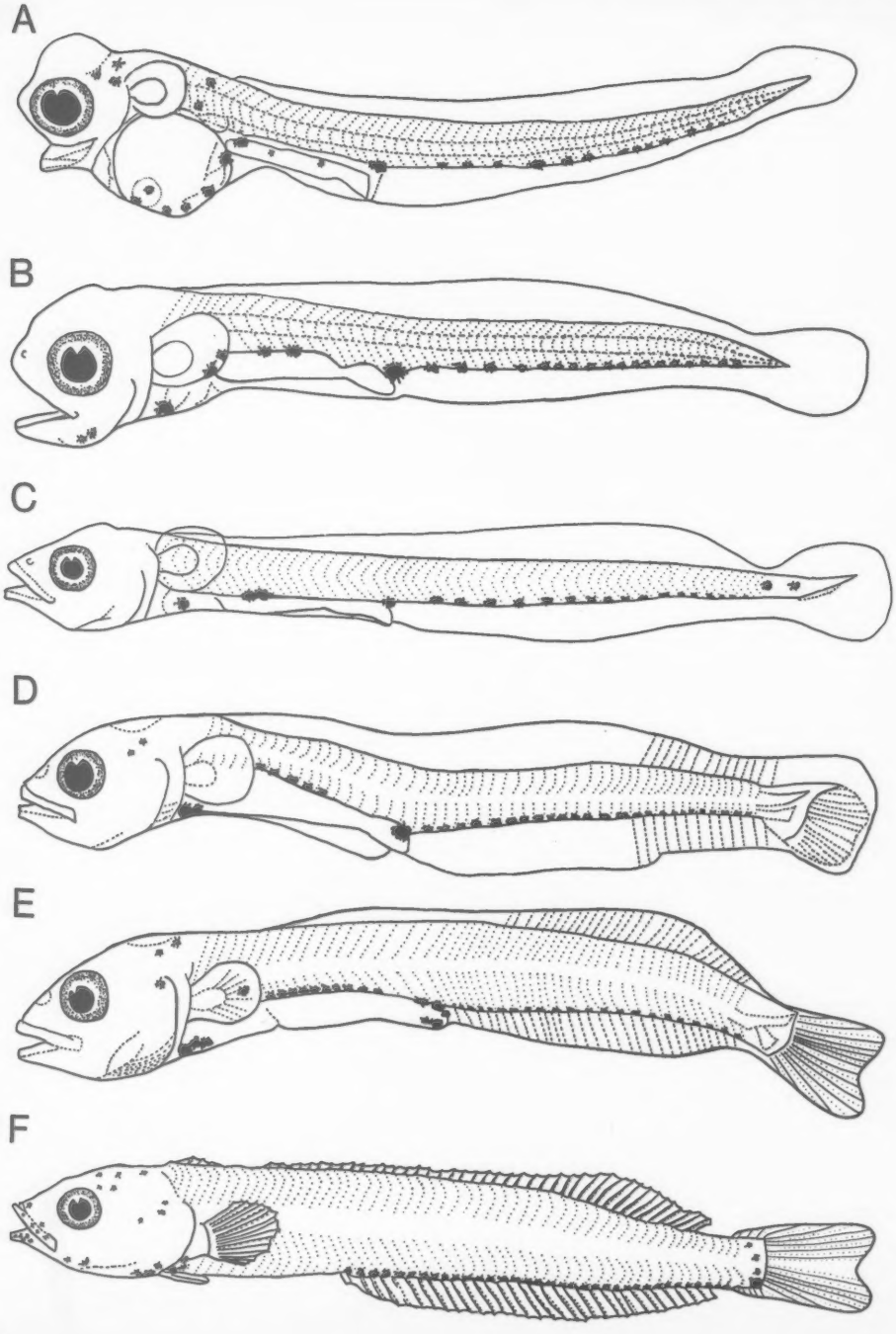
A
B
C
D
E
F

TABLE 2.—Mean sizes (TL, mm) and developmental stages of laboratory-reared giant kelpfish larvae 0-60 d.

Age[1] (d)	Mean length	Range (TL, mm)	No.	Developmental features
0	6.2	6.0-6.5	10	well-developed mouth, gut, and fin folds; 12 postanal serial melanophores
2	7.0	6.7-7.5	10	12-19 postanal melanophores, first feeding, yolk sac 1/3 original size
4	7.7	7.0-8.0	5	20 postanal melanophores, 2 melanophore spots on liver, melanophores dorsal to anus, yolk sac disappeared
6	7.9	7.4-8.4	10	some ventral caudal fin rays visible, gill rakers formed, operculum visible
7	8.3	7.5-9.0	5	notochord flexion begun in some
9	8.8	7.9-9.4	10	notochord flexion completed, swim bladder formed
11	9.7	7.9-10.7	10	caudal fin rays well-developed
13	10.3	8.2-11.2	5	schooling behavior is pronounced
15	10.9	9.5-11.7	10	fin rays in rear of dorsal and anal fin folds
17	11.4	10.0-12.3	10	scattered melanophores on top of head and lower jaw, melanophores over gut
19	11.5	10.1-12.5	5	well-developed schooling and avoidance behavior
21	11.7	10.6-13.6	10	pectoral, dorsal, and anal fin rays formed
23	12.0	11.4-14.3	10	continuous line of stellate melanophores above the gut
25	12.2	10.3-16.8	10	pelvic fins beginning to develop, melanin pigmentation in pelvic region
30	16.8	13.0-19.0	10	orange xanthophore pigmentation on top of the head, over the gut and at the base of the caudal fin; teeth visible
39	23.8	18.0-28.0	5	pelvic fins formed, 32 postanal ventral melanophores
46	25.6	22.0-27.0	10	larvae are pale gold in color
53	25.7	18.0-35.0	10	schooling no longer pronounced
60	30.6	25.0-37.0	10	most have settled onto algae

[1]Age (d) after hatching.

developed avoidance patterns and fright responses. By 5 wk, schooling was no longer as pronounced and the larvae were observed to stalk their copepod prey very efficiently.

Larval Feeding

Unless giant kelpfish larvae were given food within the first 48 h, a point of no-return was reached, after which they starved to death even if given food. Best results were obtained if larvae were fed within 24 h of hatching. *Brachionus* (rotifers) and *Tetraselmis* (algae) were found in the guts of 2-d-old larvae in the laboratory. Three-day-old larvae, even those still having yolk sacs, contained an average of 5.6 *Brachionus* and 2.9 *Tetraselmis* (Table 3). High mortality (nearly 60% of those hatched) occurred after hatching and through day 5. Dead larvae examined had apparently never eaten, despite relatively high levels of appropriately sized food items.

FIGURE 5.—Drawings of laboratory-reared giant kelpfish larvae, made with camera lucida and dissection microscope. (A) Day 0 (after hatching), 6.1 mm TL. (B) Day 4 after hatching, 7.0 mm TL. (C) Day 7 after hatching, 8.4 mm TL. (D) 2 wk, 10.9 mm TL. (E) 3 wk, 11.6 mm TL. (F) 5 wk, 22.2 mm TL.

Gut contents of field-collected kelpfish larvae (estimated to range from 0 to 9 d old) showed that they fed on a wide variety of food items, including single-celled algae, rotifers, mollusk larvae, and barnacle and copepod larvae (Table 4). Similar sizes and quantities of food items were consumed by both the laboratory-reared and field-collected larvae (Tables 3, 4).

Significantly larger food items were consumed by 2-wk-old laboratory-reared larvae, the largest widths being 52% of the mouth size (Fig. 6). Larger copepods were eaten more frequently than rotifers, although both food items were present in guts (Table 3). High mortality (ranging from 20 to 40%) also occurred at about 2.5 wk of age in both the 1980 and 1982 rearing experiments. At this age, gut examinations indicated that the larvae were switching from the smaller prey (rotifers and algae) to the larger copepods. Older larvae progressively consumed larger copepods whose size reached 70% of the mouth width by week 3 (Fig. 6, Table 3).

Settlement and Metamorphosis

After 8 wk and at a mean length of 30.6 mm, giant kelpfish larvae had well-developed, pale gold-brown pigmentation. They became increasingly thigmotac-

TABLE 3.—Gut contents of laboratory-reared giant kelpfish larvae, 3 d to 5 wk, indicating mean numbers and sizes of prey items. N = 18 (N = 3/sample). Laboratory diets 0-3 wk consisted of *Tetraselmis* and *Brachionus*. *Acartia* copepods were added to the diet at 2 wk. Sizes of kelpfish (TL, mm) and mean sizes of prey items (width × length) given.

Kelpfish larvae		Prey items					
		Tetraselmis algae		*Brachionus* rotifers		*Acartia* copepods	
Age	Size (mm)	Mean No.	Size (mm)	Mean No.	Size (mm)	Mean No.	Size (mm)
3 d	6.8 7.1 7.4	2.9	0.039 × 0.120	5.6	0.10 × 0.149	—	—
1 wk	8.0 8.2 8.2	3.3	0.050 × 0.120	14.7	0.103 × 0.157	—	—
2 wk	9.4 9.7 10.8	10.0	0.078 × 0.130	10.2	0.160 × 0.220	1.2	0.100 × 0.390
3 wk	10.7 11.5 13.6	—	—	6.8	0.130 × 0.195	2.4	0.221 × 0.520
4 wk	11.9 13.3 16.4	—	—	—	—	3.3	0.221 × 0.520
5 wk	19.7 22.0 23.0	—	—	—	—	7.9	0.220 × 0.850

TABLE 4.—Gut contents of field-collected giant kelpfish larvae 6.24-8.2 mm TL. N = 4. Mean TL of kelpfish = 6.93 mm (range 6.24-8.82 mm). Mean mouth width = 0.42 mm (0.40-0.44 mm).

Food item	Mean no./ larva	Mean width and range (mm)	Mean length and range (mm)
Diatoms	3.00	0.03 (0.01-0.07)	0.06 (0.04-0.08)
Dinoflagellates	2.00	0.03 (0.01-0.07)	0.04 (0.02-0.20)
Tintinnid protozoans	0.75	0.04 (0.03-0.07)	0.13 (0.10-0.16)
Rotifers	0.75	0.08 (0.03-0.13)	0.19 (0.08-0.35)
Barnacle nauplii and cyprids	0.75	0.10 (0.07-0.13)	0.16 (0.12-0.23)
Copepod nauplii and copepodites	3.50	0.12 (0.07-0.21)	0.40 (0.14-0.46)
Mollusk larvae	1.00	0.11 (0.09-0.12)	0.25 (0.22-0.29)
Nemertean worms	0.25	0.10	0.34
Siphonophores	0.25	0.29	0.30

tic during the next few weeks, darting amongst the artificial plants placed in their containers. Similarly, kelpfish individuals observed in situ had "settled" onto juvenile habitats by 30-50 mm TL. Juvenile habitats included the fronds of giant kelp; the brown alga, *Sargassum muticum*; and green surfgrass. Juveniles were usually in loose aggregations of three to seven similar-sized individuals until reaching a size of 7-9 cm TL.

At 5-7 cm (between 2 and 4 mo), laboratory-reared and field-collected giant kelpfish lost their transparent light gold-colored appearance, developing either green, gold, or brown pigmentation depending on their juvenile habitat, whether surfgrass, kelp, or *Sargassum*. The majority of juveniles found in surfgrass were green with striped or mottled melanin patterns and had silvery horizontal patches. Those in kelp were usually plain or mottled gold-brown with gold bellies while those in *Sargassum* developed brown pigmentation and barred or mottled melanin patterns (see Stepien 1985 and 1986 for detailed descriptions of color patterns).

Morphometrics of Larvae, Juveniles, and Adults

The SL and TL of giant kelpfish larvae were linearly related (Fig. 7). Early growth (to 40 d) of laboratory-reared larvae was logarithmic (Fig. 8A) while length and age were linearly related between 1 and 9 mo of age (Fig. 8B). Otoliths of laboratory-reared kelpfish showed abnormal ring patterns,

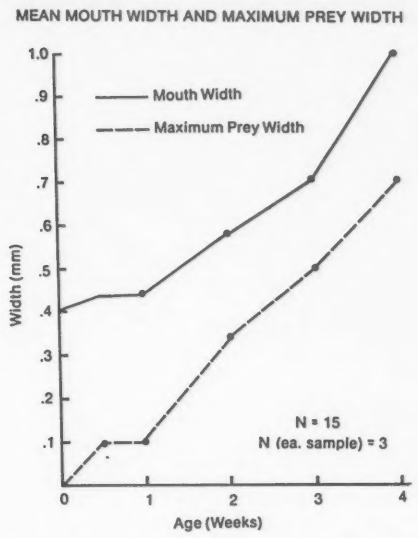

FIGURE 6.—Mean mouth width and maximum prey width consumed by laboratory-reared giant kelpfish larvae 0-4 wk old. N = 15 (N each sample = 3).

having several "checks" (false rings). Maximum age reached by laboratory-reared kelpfish in these experiments was 9 mo, at which time they succumbed to a bacterial infection.

Weight versus length of juvenile and adult kelpfish was exponentially related (Fig. 9), and SL and TL were directly linearly related (Fig. 10). Length versus age determinations also followed an exponential curve (Fig. 11). Sexual maturity occurred at a mean size of 18.6 cm TL and an age of 1-1.5 yr.

Regressions of sizes of adult males and adult females on age class were found to be significantly different using ANCOVA (see Fig. 11 legend). When sizes at given ages were compared using t-tests, females were found to be significantly larger than males at given ages past 2 yr (Fig. 12). The largest males sampled in this study were not older than 3 yr or larger than 28 cm TL. In contrast, large females, reaching ages of 4.5 yr and sizes of 42 cm (TL) were collected. Larger individuals collected throughout the 5-yr sampling regime were consistently females.

Population Structure

Seasonal size class structure of the giant kelpfish population was consistent over 2 yr of regular sam-

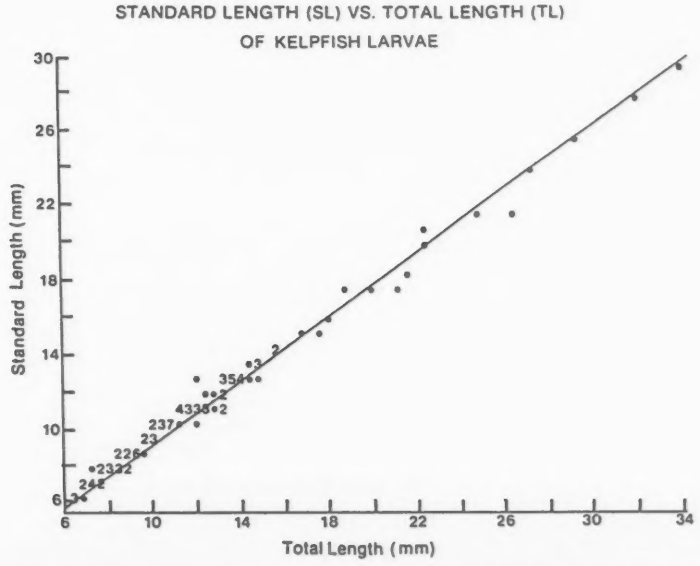

FIGURE 7.—SL (mm) versus TL (mm) of laboratory-reared giant kelpfish larvae 0-30 d old. * = one fish. N = 108. Regression equation: SL = 0.598 + 0.819 (TL). F = 11,588.62, $P < 0.00001$.

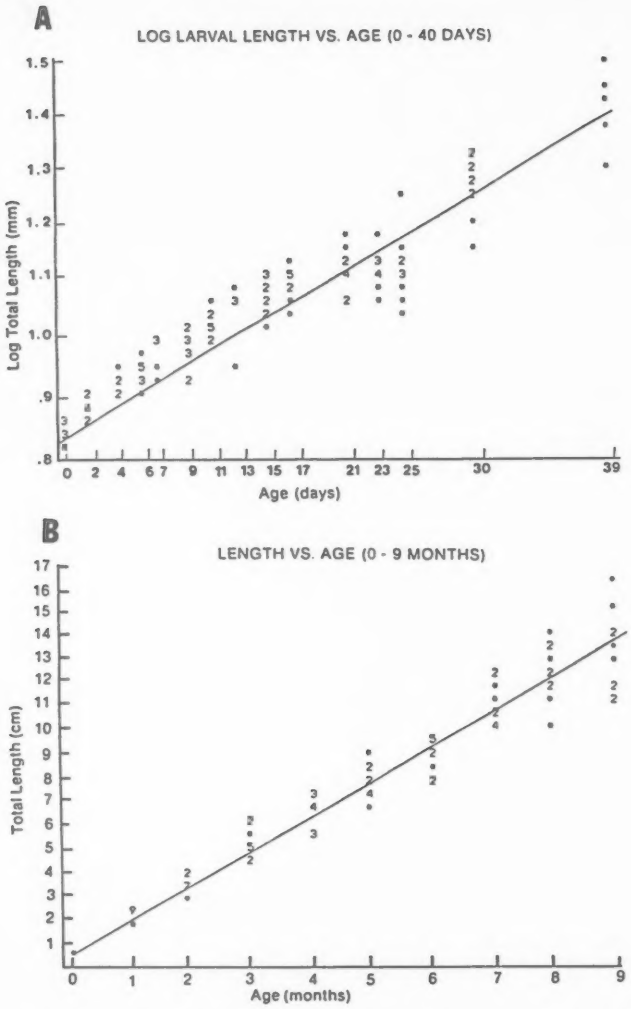

FIGURE 8.—(A) Log length (TL, mm) versus age (0-40 d) of laboratory-reared giant kelpfish larvae. * = one fish. N = 130. Regression equation: Log TL = 0.814 + 0.013 (days). F = 1,211.9, $P < 0.0001$. (B) Growth of laboratory-reared giant kelpfish (0-9 mo), length (cm) versus age (months). * = one fish. N = 100. Regression equation: TL = 0.379 + 1.482 (months). F = 2,230.8, $P < 0.0001$.

pling (Fig. 13). Contingency tests of independence showed that numbers of individuals in various size classes differed significantly with season in 1981-82 and 1982-83. Juveniles appeared in significant numbers during the spring and summer months. These data agreed with observations on spawning and appearance of larvae in the water column, indicating that most Catalina Island kelpfish in these years spawned from January through May. During spring and summer, a large portion of the population was estimated to be 1 and 2 yr old, composed of individuals of reproductive age. During the fall

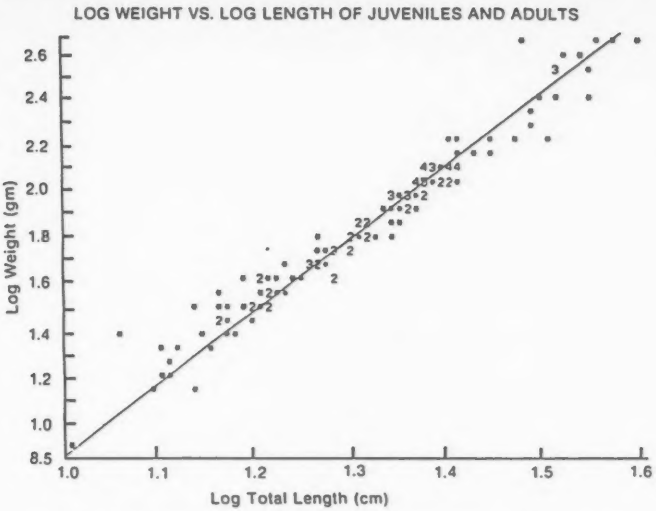

FIGURE 9.—Log weight (g) versus log TL (cm) of juvenile and adult giant kelpfish. * = one fish. N = 140. Regression equation: Log weight = −2.508 + 3.243 (log TL). F = 3,622.7, P < 0.0001.

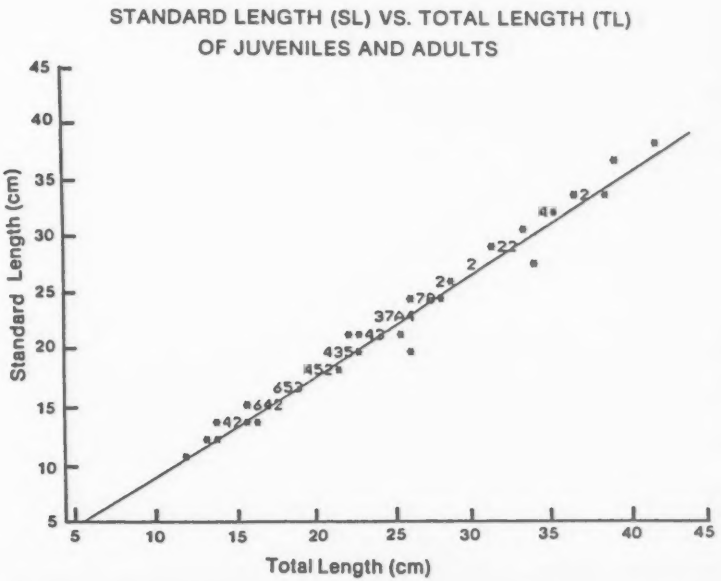

FIGURE 10.—SL (cm) versus TL (cm) of juvenile and adult giant kelpfish. * = one fish. A = 11 fish. N = 140. Regression equation: SL = −0.580 + 0.906 (TL). F = 15,993.0, P < 0.0001.

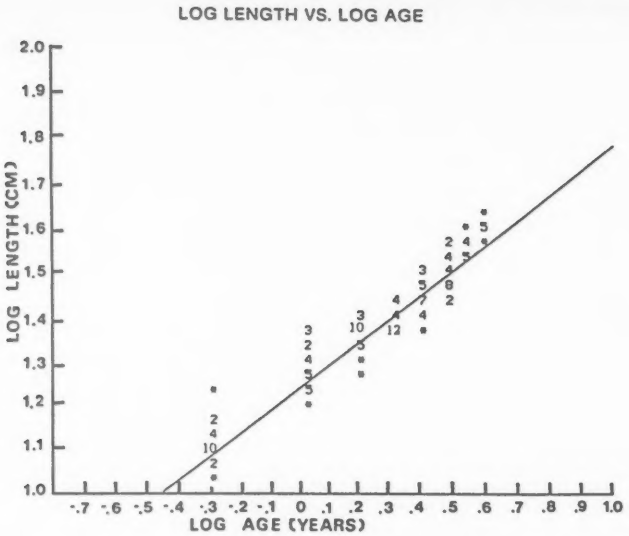

FIGURE 11.—Log TL (cm) versus log age class (years) of juvenile and adult giant kelpfish (males and females). * = one fish. N = 137. Regression equation: Log TL = 1.234 + 0.528 (log age). F = 1,589.28, $P < 0.0001$. Regression equation for females only (N = 77): Log TL = 1.234 + 0.561 (log age); F = 1,460.7, $P < 0.0001$. Regression equation for males only (N = 60): Log TL = 1.235 + 0.453 (log age); F = 535.0, $P < 0.001$. ANCOVA regression analysis of log TL for males and females (two different groups versus log age class (years): F = 5.82 ($P < 0.05$).

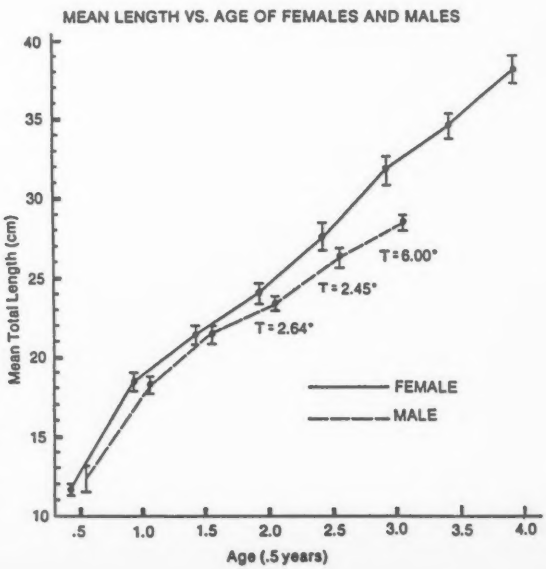

FIGURE 12.—Mean TL (cm) versus age class (years) of female and male giant kelpfish. Significant differences between male and female mean sizes indicated. * = Significant difference in t-test results (0.05 level). Standard error bars shown. N = 137. Two-way ANOVA with replication for mean lengths of male and female kelpfish at three ages (2.0, 2.5, and 3.0 yr) showed significant differences between the sexes (F = 38.52, $P < 0.001$) and the age classes (F = 78.01, $P < 0.001$), but no interaction (sex x ages; F = 3.37).

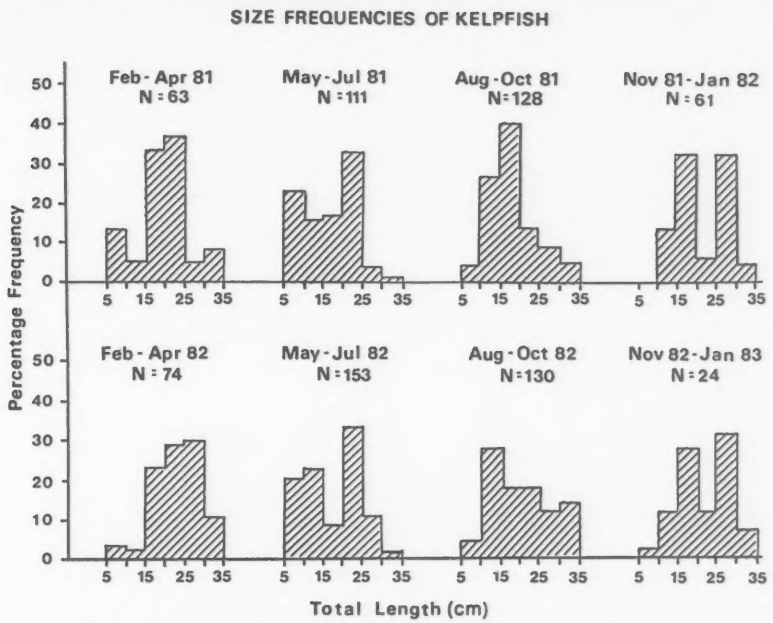

FIGURE 13.—Percentage frequencies of giant kelpfish size classes collected seasonally from February 1981 to January 1983. N = 744. Contingency table R × C *G* tests of independence showed significant seasonal variations in frequencies of kelpfish size classes in 1981-82 ($N = 363$; $\chi^2 = 167.73$, 15 df, $P < 0.001$) and 1982-83 ($N = 381$; $\chi^2 = 86.07$, 15 df; $P < 0.001$). (Sokal and Rohlf 1981.)

months, the most abundant size classes were estimated as 0.5 and 1.5 yr of age. These size frequencies also indicate that a relatively low percentage of the population is composed of individuals 3 yr and older.

DISCUSSION

Reproduction and Development

Unlike *Heterostichus*, whose nests contain eggs in similar stages of development, those of the fringehead *Neoclinus bryope* (family Clinidae; subfamily Chaenopsidae) contain various developmental stages, apparently from several spawnings (Shiogaki and Dotsu 1972). *Heterostichus* eggs have a single large oil globule (see Barnhart 1932 and Figure 3C), while other described clinid eggs have several (Sparta 1948; Shiogaki and Dotsu 1972; Matarese et al. 1984). Unfertilized eggs of *Gibbonsia elegans* contain a mass of 6-16 small oil globules (Stepien[3]). Like *Heterostichus* (see Figure 3D), *Clinus argentatus* eggs develop large black melanophores over the surface (Sparta 1948).

Early larval development in other clinids resembles that of *Heterostichus*, although few species have been studied and none have been reared past the yolk-sac stage. Other clinids are reported to hatch at similar sizes and at comparable development (Sparta 1948; Shiogaki and Dotsu 1972; Matarese et al. 1984). As in *Heterostichus*, the yolk-sac stage persists for 2-3 d (Shiogaki and Dotsu 1972), caudal fin rays develop first (Matarese et al. 1984), and dorsal and anal fin rays form posteriorly to anteriorly (Risso 1948; Shiogaki and Dotsu 1972; Matarese et al. 1984). Flexion of the notochord appears to occur at a smaller size in *Heterostichus* (mean 8.5 mm TL) than in some other clinids (by 11.1 mm TL in *Neoclinus* and 11.52 mm TL in *Clinus argentatus*) (Sparta 1948; Shiogaki and Dotsu 1972).

[3]Stepien, C. A. 1986b. Life history of the spotted kelpfish, *Gibbonsia elegans* Cooper. Unpubl. manuscr. Marine Biology Research Division A-002, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093.

Swimming behavior of newly hatched kelpfish larvae, characterized by short periods of swimming interspersed with longer periods of inactivity, is common in many small marine yolk-sac larvae (Hunter 1972; Ellertsen et al. 1980; Weihs 1980). Like kelpfish, some other newly hatched larvae including cod, *Gadus morhua*, (Ellertsen et al. 1980) and white seabass, *Atractoscion* (*Cynoscion*) *nobilis*, (Orhun[4]) swim upside-down for the first 24 h after hatching. This behavior is due to positive buoyancy of the yolk (Hunter[5]). Kelpfish larvae, in situ as well as in the laboratory, schooled between 2 wk and 2 mo of age. Larval schooling is common in species of nearshore fishes which also school as adults (Smith 1981; Hunter 1981) and may serve to increase the probability of locating patches of food and/or may help them avoid predation. No reference to larval schooling in fishes that do not school as adults was found in the literature.

Larval Feeding

A point of no-return at which starvation occurs even if larvae are fed appears to occur earlier in giant kelpfish (after 36 h) than in fish larvae hatching from pelagic eggs (Hunter 1981) and is probably due to their greater degree of development at hatching (i.e., smaller yolks and well-developed mouths and digestive tracts). Only a small number of species are sufficiently developed to consume exogenous food shortly after hatching (Balon 1984a, b). Early feeding during the yolk-sac stage may be critical for the larvae to develop a "search" image and capture skills (Hunter 1981).

In this study, high mortality following the yolk-sac stage was apparently due to starvation, despite relatively high levels of appropriate-sized food items. In many marine fishes, relatively low feeding success is apparently common in field-collected, as well as laboratory-reared, larvae (Hunter 1981). During the first week, field-collected, as well as the laboratory-reared, larvae consume a wide variety of food items, primarily smaller ones such as unicellular algae. Like *Heterostichus*, most species of larval fishes have been found to eat many more small prey items than larger ones (Hunter and Kimbrell 1980; Hunter 1981).

High mortality also occurred in the laboratory at about 2.5 wk, when larvae were apparently switching from smaller to larger prey. This may be a critical period when the larvae have to learn to capture larger, faster swimming crustaceans as the primary dietary component in order to obtain sufficient caloric intake. Studies on other fish larvae have demonstrated the necessity of increasing prey size with growth (Hunter 1977; Hunter and Kimbrell 1980).

Juvenile and Adult Life History

Ages of juveniles and adults calculated in the present study agree with estimates for giant kelpfish determined by J. E. Fitch (in Feder et al. 1974) and by R. Collins[6]. Ages by Coyer (1982), based on 42 kelpfish samples, do not agree with those in the present study. Coyer appeared to have overestimated the oldest kelpfish by 3 yr. This may have been due to the prevalence of "checks" or partially completed false rings on the otoliths which are commonly formed during spawning (Collins and Spratt 1969) and were frequently observed in the present study. Estimated size at sexual maturity (mean 18.6 cm TL) agrees with that reported by Coyer (1982).

Past the age of sexual maturity, female giant kelpfish are significantly larger than males and also live several years longer. Size discrepancy between adult males and females may have evolved from the females' behavior of venturing away from their territories during the spring spawning season into those occupied by males (Stepien 1985, 1986). They are often readily visible at this time while away from plants of matching colors. Large size may help females to avoid predation or, alternatively, may be the result of selection for increased fecundity.

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[4]Orhun, R. M. 1986. Culture and growth of larval and early juvenile white seabass, *Atractoscion* (*Cynoscion*) *nobilis*. M.S. Thesis in preparation, Center for Marine Studies, Department of Biology, San Diego State University, San Diego, CA 92182.

[5]John Hunter, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun. January 1986.

[6]Robson Collins, California State Department of Fish and Game, Long Beach, CA 90813, pers. commun. March 1982.

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LITERATURE CITED

BALON, E. K.
1984a. Reflections on some decisive events in early life of fishes. Trans. Am. Fish. Soc. 113:178-185.
1984b. Patterns in the evolution of reproductive styles in fishes. *In* G. W. Potts and R. J. Wooton (editors), Fish reproduction: strategies and tactics, p. 35-53. Acad. Press, Lond.

BARNHART, P. S.
1932. Notes on the habits, eggs, and young of some fishes of southern California. Bull. Scripps Inst. Oceanogr., Univ. Calif. 3:87-99.

COLLINS, R. A., AND J. D. SPRATT.
1969. Age determination of northern anchovies, *Engraulis mordax*, from otoliths. Calif. Fish Bull. 147:39-55.

COYER, J. A.
1979. The invertebrate assemblage associated with *Macrocystis pyrifera* and its utilization as a food resource by kelp-forest fishes. Unpubl. Ph.D. Thesis, Univ. Southern California, Los Angeles, 314 p.
1982. Observations on the reproductive behavior of the giant kelpfish, *Heterostichus rostratus* (Pisces: Clinidae). Copeia. 1982:344-350.

ELLERTSEN, B., P. SOLEMDAL, T. STROMME, S. TILSETH, T. WESTGARD, E. MOKSNESS, AND V. OIESTAD.
1980. Some biological aspects of cod larvae (*Gadus morhua* L.). Fiskeridir. Skr. Ser. Havunders. 17:29-47.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Fish Bull. 160:1-144.

FITCH, J. E.
1951. Age composition of the southern California catch of Pacific mackerel 1939-40 through 1950-51. Calif. Fish Bull. 83:1-75.

HOBSON, E. S.
1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.

HOBSON, E. S., W. N. MCFARLANE, AND J. R. CHESS.
1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. Fish. Bull., U.S. 79:1-30.

HOLDER, C. F.
1907. The nest of the kelpfish. Am. Nat. 41:587-588.

HOUDE, E. D.
1972. Some recent advances and unsolved problems in the culture of marine fish larvae. Proc. World Maricult. Soc. 3:83-112.

HUBBS, C.
1952. A contribution to the classification of the Blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. Stanford Ichthyol. Bull. 4:41-165.

HUBBS, C. L.
1920. Protective coloration and habits in the kelpfish, *Heterostichus rostratus*. Copeia 1920:19-20.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1977. Behavior and survival of northern anchovy *Engraulis mordax* larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 19: 138-146.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology, and relation to fisheries, p. 33-77. Wash. Sea Grant Program, Seattle.

HUNTER, J. R., AND C. A. KIMBRELL.
1980. Early life history of Pacific mackerel, *Scomber japonicus*. Fish. Bull., U.S. 78:89-101.

JENSEN, A. C.
1965. A standard terminology and notation of otolith readers. Int. Comm. Northwest Atl. Fish. Res. Bull. 2:5-7.

LIMBAUGH, C.
1955. Fish life in the kelp beds and the effects of kelp harvesting. Inst. Mar. Res. Ref. 55-9, 158 p.

MATARESE, A. C., W. WATSON, AND E. G. STEVENS.
1984. Blennioidea: Development and relationships. *In* H. G. Moser et al. (editors), Ontogeny and systematics of fishes, p. 565-577. Am. Soc. Ichthyol. Herpetol. Spec. Pub. 1.

QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109-142. Bull. Calif. Dep. Fish Game 139.

ROEDEL, P. M.
1953. Common ocean fishes of the California coast. Calif. Fish Bull. 91:1-184.

SHIOGAKI, M., AND Y. DOTSU.
1972. The life history of the blenniid fish, *Neoclinus bryope*. [In Jpn., Engl. abstr.] Bull. Fac. Fish. Nagasaki Univ. 34, p. 1-8.

SMITH, P. E.
1981. Fisheries on coastal pelagic schooling fish. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology, and relation to fisheries, p. 1-31. Wash. Sea Grant Program, Seattle.

SOKAL, R. R., AND F. J. ROHLF.
1981. Biometry: The principle and practice of statistics in biological research. 2d ed. W. H. Freeman and Co., San Franc., 859 p.

SPARTA, A.
1948. Uova ovariche, uova fecondate tenute in colture larva alla schiusa, stadi larvali e giovanile di *Cristiceps argenatus*. Risso. [In Ital.] Arch. Oceanogr. Limnol., Mem. 315 (1-3): 79-84.

STEPIEN, C. A.
1985. Life history, ecology, and regulation of the colormorphic patterns of the giant kelpfish *Heterostichus rostratus* Girard (Family Clinidae). Ph.D. Thesis, Univ. Southern California, Los Angeles, 318 p.

1986. Regulation of the colormorphic patterns in the giant kelpfish, *Heterostichus rostratus* Girard: Genetic versus environmental factors. J. Exp. Mar. Biol. Ecol. 100:181-208.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

WEIHS, D.
1980. Energetic significance of changes in swimming modes during growth of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:597-604.

ZIMMERMAN, R. C., AND J. L. KREMER.
1983. Crunch: The friendly data analysis program. Zimmerman and Kremer, Los Ang., 17 p.

A SIMPLE METHOD FOR ESTIMATING THE FOOD CONSUMPTION OF FISH POPULATIONS FROM GROWTH DATA AND FOOD CONVERSION EXPERIMENTS[1]

DANIEL PAULY[2]

ABSTRACT

Experimental data on the gross food conversion efficiency of fishes (K_1 = growth increment/food ingested) are usually reduced to a model of the form $K_1 = aW^b$; it is shown that the model $K_1 = 1 - (W/W_\infty)^\beta$ has a number of advantages over the traditional model.

The new model can be used to compute the food consumption per unit biomass of an age-structured fish population, by relying on the first derivative of the von Bertalanffy growth formula (VBGF) to express growth increments, and the identity of W_∞ in the VBGF and in the model expressing K_1 as a function of weight.

Computed examples, using published growth and mortality parameters, and the results of food conversion experiments were used to obtain consumption estimates in a carnivorous grouper (*Epinephelus guttatus*) and an herbivorous angelfish (*Holacanthus bermudensis*). Results were shown to be most sensitive to the parameter β. Various applications of this simple model are discussed, particularly as a method to estimate key inputs in J. J. Polovina's ECOPATH model.

A multiple-regression extension of the basic model is presented which accounts for the impact of factors other than body weight on values of K_1 and β. This method is illustrated with an analysis of data on dab (*Limanda limanda*).

Estimating the quantity of food eaten during a certain period by a fish population from field data is usually a difficult task and various sophisticated methods developed for this purpose have data requirements which can make their routine application impossible (Beverton and Holt 1957; Ursin 1967; Daan 1973, 1983; Andersen 1982; Armstrong et al. 1983; Rice et al. 1983; Stewart et al. 1983; Pennington 1984; Majkowski and Hearns 1984). Polovina (1984) recently presented a technique for construction of ecosystem models which is structured around a well-documented computer program called ECOPATH (Polovina and Ow[3]). In situations where classical fishery data are sparse this technique has the potential of becoming a standard method for consolidating and examining the data available on aquatic ecosystems. ECOPATH estimates equilibrium biomass (B), annual production (P), and annual consumption (Q) for each group in the model. ECOPATH requires a number of data inputs for each group treated in the model and usually the most difficult to obtain is the average food consumption per unit biomass (Q/B) of each group. The present study derives a method to estimate Q/B through a combination of experimental and field data that are easily obtained. In the process, a model is derived which will allow for more information to be extracted from feeding experiments than has hitherto been the case.

MODEL FOR REDUCING EXPERIMENTAL DATA ON THE CONVERSION EFFICIENCY OF FISHES

Usually laboratory or pond feeding experiments lead to estimates of K_1, the gross conversion efficiency, which are obtained, for short intervals, from

$$K_1 = \text{growth increment/food ingested} \quad (1)$$

(Ivlev 1939, 1966).

Usually, K_1 declines with body size (other factors affecting K_1 are discussed below) and it has become

[1]Based on Chapter 3 of a "Habilitationschrift" presented in December 1984 to the Dean of the Mathematics and Science Faculty, Kiel University (Federal Republic of Germany) and titled "Zur Biologie tropischer Nutztiere: eine Bestandsaufnahme von Konzepten und Methoden." ICLARM Contribution No. 281.

[2]International Center for Living Aquatic Resources Management, MCC P.O. Box 1501, Makati, Metro Manila, Philippines.

[3]Polovina, J. J., and M. D. Ow. 1983. ECOPATH: a user's manual and program listings. Southwest Fish. Cent. Admin. Rep. H 82-83. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

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a standard procedure to plot empirical values of K_1 obtained against the corresponding body weights, i.e., the mean weights (W) corresponding to each growth increment, or

$$\log_{10} K_1 = \log_{10} a + b \log_{10} W \quad (2)$$

which leads to the model

$$K_1 = aW^b. \quad (3)$$

(See Sprugel 1983 for a method to correct the bias due to log transformation in this and the other models below.) A discussion of this model may be found in Jones (1976) (see Figure 1a for an example).

This model has three liabilities, the first of which is the most serious:

1) The parameters "a" and "b" have no biological meaning, i.e., cannot be predicted from one's knowledge of the biology of a given fish. Converse-

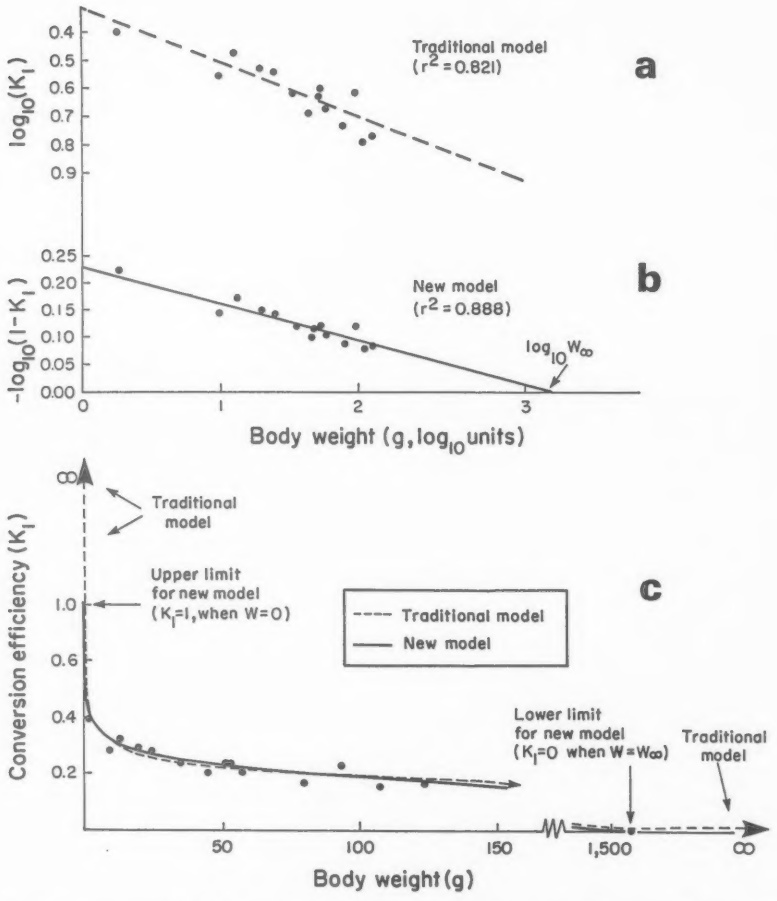

FIGURE 1.—Relationship of gross food conversion efficiency (K_1) and body weight (W) in *Channa striata*. a) Plot of $\log_{10}K_1$ on $\log_{10}W$, as needed to estimate parameters "a" and "b" of traditional model for prediction of K_1 from body weight. b) Plot of $-\log_{10}(1-K_1)$ on $\log_{10}W$, as needed to estimate parameters W_∞ and β of new model. c) Comparison of the two models. Note that both fit the data well over the range for which data points are available, but that the traditional model provides nonsensical results beyond this range (see text). Based on the data in Pandian (1967).

ly, these parameters do not provide information which can be interpreted via another model.

2) The model implies values of $K_1 > 1$ when $a^{-1/b} > W > 0$, which is nonsensical.

3) The model implies that, except when $W = 0$, K_1 is always > 0, even in very large fish, although it is known that fish cannot grow beyond certain species-specific and environment-specific sizes, whatever their food intake.

The new model proposed here has the form

$$K_1 = 1 - (W/W_\infty)^\beta \qquad (4)$$

with β as a constant and W_∞ as the weight at which $K_1 = 0$. The model implies that $K_1 = 1$ when $W = 0$, whatever the values of β and W_∞ (see Discussion for comments on using values other than 1 as upper bound for K_1 in Equation (4)). The new model can, as the traditional model, be fitted by means of a double logarithmic plot:

$$C = \beta \log_{10} W_\infty - \beta \log_{10} W \qquad (5)$$

where $C = -\log_{10}(1 - K_1)$, the sign being changed here to allow the values of C to have the same positive sign as the original values of K_1. Interestingly, it also appears that negative values of K_1 (based on fish which lost weight), which must be ignored in the traditional model, can also be used in this model (as long as they do not drag the mean of all available K_1 values below zero, see Table 1), although their interpretation seems difficult.

The new model requires no more data, nor markedly more computations than the old one. It produces "possible" values of K_1 over the whole range of weights which a given fish can take. The values of W_∞, which represent the upper bound of this range can be estimated from

$$W_\infty = \text{antilog}_{10}(C \text{ intercept}/|\text{slope}|). \qquad (6)$$

Thus, while β has no obvious biological meaning, the values of W_∞ obtained by this model do have a biological interpretation, which is, moreover, analogous to the definition of W_∞ in the von Bertalanffy growth function (VBGF) of the form

TABLE 1.—Data on the food conversion efficiency of *Channa striata* (= *Ophiocephalus striatus*) (after Pandian 1967), *Epinephelus striatus* (after Menzel 1960), and *Holacanthus bermudensis* (after Menzel 1958).

Body weight (g)[1]	Food conv. (K_1)[2]	Transformed data		$C = -\log_{10}(1-K_1)$	Species and remarks
		$\log_{10} W$	$\log_{10} K_1$		
1.86	0.391	0.270	−0.408	0.215	
9.92	0.274	0.998	−0.562	0.139	
13.09	0.320	1.117	−0.495	0.167	
19.65	0.284	1.293	−0.547	0.147	
24.63	0.278	1.391	−0.556	0.141	
35.09	0.234	1.545	−0.631	0.116	
45.15	0.199	1.655	−0.701	0.096	*Channa striata*
50.70	0.227	1.705	−0.644	0.112	(see Figure 1)
51.30	0.235	1.710	−0.629	0.116	
57.00	0.208	1.756	−0.682	0.101	
79.80	0.177	1.897	−0.752	0.085	
93.80	0.232	1.972	−0.635	0.115	
107.50	0.157	2.031	−0.804	0.074	
123.80	0.166	2.093	−0.780	0.079	
216	0.247	2.334	−0.607	0.123	
285	0.219	2.455	−0.600	0.107	*Epinephelus guttatus*;
319	0.160	2.504	−0.796	0.076	$\overline{\log_{10} W} = 2.617$;
392	0.153	2.593	−0.815	0.072	$\bar{C} = 0.0894$
424	0.179	2.627	−0.747	0.086	(see Figure 2)
628	0.161	2.798	−0.793	0.076	
647	0.177	2.811	−0.752	0.085	
649	0.187	2.812	−0.728	0.090	
66	0.222	1.820	−0.654	0.109	*Holacanthus bermudensis* (28°C only)[3]
139	0.178	2.143	−0.750	0.085	
256	−0.258	2.408	not defined	−0.100	$\overline{\log_{10} W} = 2.124$
					$\bar{C} = 0.031$

[1]Mean of starting and end weights.
[2]Growth increment/food intake.
[3]Note that the experiment considered here was conducted with a food which led to deposition of fat, but not of protein (see also Table 2), a consideration that is ignored for the sake of this example.

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \quad (7)$$

(von Bertalanffy 1938; Beverton and Holt 1957), and where W_t, the weight at time t, is predicted via the constants K, t_0, and W_∞, all three of which are usually estimated from size-at-age data obtained in the field (see Gulland 1983 or Pauly 1984a).

That W_∞ values obtained via Equations (2) and (6) are realistic can be illustrated by means of that part of the data in Table 1 pertaining to *Channa striata* (= *Ophiocephalus striatus*), the "snakehead" or "mudfish" of south and southeast Asia. These data give, when fitted to the traditional model

$$K_1 = 0.482W^{-0.205}. \quad (8)$$

The same data, when fitted to the new model give

$$K_1 = 1 - (W/1{,}580)^{0.073}. \quad (9)$$

(See Figure 1 for both models.) The value of W_∞ = 1,580 g is low for a fish which can reach up to 90 cm in the field (Bardach et al. 1972). However, its growth may have been reduced in laboratory growth experiments conducted by Pandian (1967).

Equation (6) used here to predict W_∞ is extremely sensitive to variability in the data set investigated, and two approaches are discussed to deal with this problem.

The first approach is the appropriate choice of the regression model used. In the example above (Equation (9)), the model used was a Type I (predictive) regression, which is actually inappropriate, given that

1) the $\log_{10} W$ values are not controlled by the experimentator and
2) regression parameters are required, rather than prediction of C values (see Ricker 1973).

The use of a Type II ("functional", or "Geometric Mean") regression appears more appropriate; conversion of a Type I to Type II regression (with parameters a', b') can be performed straightforwardly through

$$b' = b/|r| \quad (10)$$

and

$$a' = \bar{C} - b' \overline{\log_{10} W} \quad (11)$$

where r is the correlation coefficient between the C and the $\log_{10} W$ values (Ricker 1973). In the case of the example here, one obtains with r = 0.942 a new model:

$$K_1 = 1 - (W/1{,}290)^{0.077} \quad (12)$$

close to that obtained using a Type I regression, due to the high value of r of this example. However, in cases where the fit to the model is poor, the use of a Type II regression can make all the difference between realistic and improbable values of W_∞.

Another approach toward optimal utilization of the properties of the new model (4) is the use of "external" values of asymptotic weight, which will here be coded $W_{(\infty)}$ to differentiate them from values of W_∞ estimated through the model. In such case, β can be estimated from

$$\beta = \bar{C}/(\log_{10} W_{(\infty)} - \overline{\log_{10} W}) \quad (13)$$

in which $W_{(\infty)}$ is an asymptotic size estimated from other than food conversion and weight data, e.g., from growth data or via the often observed closeness between estimates of asymptotic size and the maximum sizes observed in a given stock (see Pauly 1984a, chapter 4).

These two approaches are illustrated in the example below, which is based on the data in Table 1 pertaining to the grouper *Epinephelus guttatus*. When Equation (6) is interpreted as a Type I regression, these data yield a value of $W_\infty > 12$ kg, which is far too high for a fish known to reach 55 cm at most (Randall 1968). Interpreting Equation (5) as a Type II regression leads to a value of W_∞ = 3.5 kg which is realistic, although still not close to the asymptotic weight of 1,880 g estimated by Thompson and Munro (1977). Finally, using the latter figure as an estimate of $W_{(\infty)}$ yields the model

$$K_1 = 1 - (W/1{,}880)^{0.136} \quad (14)$$

as a description of the relationship between K_1 and weight in *Epinephelus guttatus* (Fig. 2). The value of β in Equation (14) lies within the 95% confidence interval of the value of β = 0.060 which generated the first unrealistically high estimate of W_∞.

MODEL FOR ESTIMATING THE FOOD CONSUMPTION OF FISH POPULATIONS

When feeding experiments have been or can be conducted under conditions similar to those prevailing in the sea (food type, temperature, etc.), the

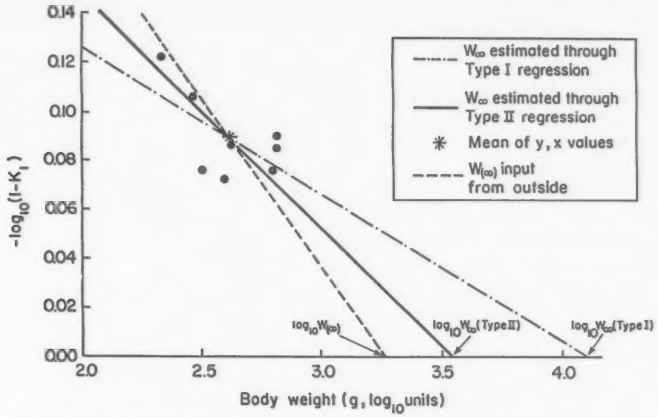

FIGURE 2.—Relationship between gross food conversion efficiency (K_1) and body weight in *Epinephelus guttatus*. Note that a Type I "predictive" regression leads to an overestimation of W_∞ while a Type II "functional" regression leads to a value of W_∞ close to an estimate of W_∞ based on growth data (see text). Based on data in Menzel (1960).

model presented above can be made a part of a model for estimation of food consumption per unit biomass (Q/B), provided a set of growth parameters is also used in which the value of W_∞ or $W_{(\infty)}$ is identical to that estimated from or used to interpret the feeding experiments.

In this case, inserting Equation (8) into Equation (5) leads to

$$K_{1(t)} = 1 - (1 - e^{-K(t-t_0)})^{3\beta} \tag{15}$$

where $K_{1(t)}$ is the food conversion efficiency of the investigated fish as a function of their age t, and K, t_0, and β are as defined above.

Equation (1) is then rewritten as

$$dq/dt = (dw/dt)/K_{1(t)} \tag{16}$$

where the "growth increment" is replaced by a growth rate (dw/dt) and the "food ingested" is also expressed as a rate (dq/dt). The growth rate of the fish is then expressd by the first derivative of the VBGF (Equation (7)) or

$$dw/dt = W_\infty\, 3K\,(1 - \exp(-Kr_1))^2 \cdot \exp(-Kr_1) \tag{17}$$

where $r_1 = t - t_0$. Equations (17) and (15) may be substituted into Equation (16), which is a separable differential equation and may be solved by direct integration. The cumulative food consumption of an individual fish between the age at recruitment (t_r) and the age at which it dies (t_{max}) is thus

$$Q_c = W_\infty\, 3K \int_{t_r}^{t_{max}} \frac{(1 - \exp(-Kr_1))^2 \cdot \exp(-Kr_1)}{1 - (1 - \exp(-Kr_1))^{3\beta}}\, dt. \tag{18}$$

The food consumption of a population should depend, on the other hand, on the age structure of that population. The simplest way to impose an age structure on a population is to assume exponential decay with instantaneous mortality Z, or

$$N_t = R\, e^{-Z(t-t_r)} \tag{19}$$

where t_r is the age at recruitment (i.e., the starting age at which Z applies, assuming, if there is any fishery, that $t_r = t_c$, the mean age at first capture), R the number of recruits, and N_t is the number of fish in the population. As the model below assumes a stationary population, the food consumption of the population per unit time can be expressed on a per-recruit basis or

$$\frac{Q}{R} = W_\infty\, 3K \int_{t_r}^{t_{max}} \frac{(1 - \exp(-Kr_1))^2 \cdot \exp(-(Kr_1 + Zr_2))}{1 - (1 - \exp(-Kr_1))^{3\beta}}\, dt \tag{20}$$

where $r_2 = t - t_r$.

The biomass per recruit in fish whose growth can be described by Equation (7) is, according to the model of Beverton and Holt (1957; see also Ricker 1975, p. 253):

$$\frac{B}{R} = W_\infty (A_1 + A_2 + A_3 + A_4) \qquad (21)$$

where $A_1 = \dfrac{1 - e^{-Zr_3}}{Z}$

$$A_2 = \frac{-3\, e^{-Kr_4}\left(1 - e^{-(Z+K)r_3}\right)}{Z + K}$$

$$A_3 = \frac{3\, e^{-2Kr_4}\left(1 - e^{-(Z+2K)r_3}\right)}{Z + 2K}$$

and

$$A_4 = \frac{-\, e^{-3Kr_4}\left(1 - e^{-(Z+3K)r_3}\right)}{Z + 3K}$$

where $r_3 = t_{max} - t_r$

$$r_4 = t_r - t_0.$$

This model assumes, as does Equation (20), a stable age distribution.

Combining Equations (21) and (20) leads to the model for estimating Q/B, which has the form:

$$\frac{Q}{B} = \frac{3K \displaystyle\int_{t_r}^{t_{max}} \frac{(1 - \exp(-Kr_1))^2 \cdot \exp(-(Kr_1 + Zr_2))}{1 - (1 - \exp(-Kr_1))^{3\beta}}\, dt}{(A_1 + A_2 + A_3 + A_4)}. \qquad (22)$$

Equation (22) has only 6 parameters (K, t_0, t_r, t_{max}, Z, and β); of these, K and t_0 are estimated from growth data, while t_r and t_{max} can be set more or less arbitrarily (see text below and Figure 3). Total mortality (Z), which is here the equivalent of a production/biomass ratio (see Allen 1971) can be estimated easily, e.g., from length-frequency data and growth parameters (see Pauly 1982, 1984a: chapter 5) and is an input required anyway by the ECOPATH program (Polovina 1984). Thus only β and a "hidden" value of W_∞ applicable to both food experiment and growth data are needed in addition to the easily obtainable parameters required by this model.

APPLICATION EXAMPLE AND SENSITIVITY ANALYSIS OF THE MODEL

In the following application examples, the newly derived model (Equation (22)) is used to compare the food consumption of a tropical carnivore (*Epinephelus guttatus*) with that of a tropical herbivore (*Holacanthus bermudensis*). A list of the parameter values used is given on Table 2.

The solutions of Equation (22), inclusive of the integration of its numerator, were obtained by means of a short BASIC microcomputer program available from me. Note that the integration, which according to Equation (22) should be performed for the interval between two ages (t_r and t_{max}), can be performed for the intervals between two sizes (W_r, W_{max}), the age corresponding to these sizes being estimated from the inverse of Equation (7), i.e.,

$$t = t_0 - ((1/K)\,(\log_e (1 - W/W_\infty)^{1/3})). \qquad (23)$$

The results, i.e., the values of Q/B, expressed as a percentage on a daily basis are 0.76 for *E. guttatus* and 2.50 for *H. bermudensis*.

A sensitivity analysis of Equation (22) was performed, following the outline in Majkowski (1982). The results are given in Figure 3, which shows that of the six parameters of Equation (22), β is the one which has the strongest impact on the estimates of Q/B, while t_r has the least, the relationships between the importance of these parameters being best summarized by

$$\beta > K > Z >> t_{max} > t_0 > t_r \qquad (24)$$

These results suggest that, when using this model, most attention should be given to an accurate estimation of β (see below). It should be also noted that β and K have opposite effects on the estimation of Q/B (see Figure 3). Thus, a biased (e.g., high) estimate of W_∞ will be associated with too low values of β and K which partially compensate each other.

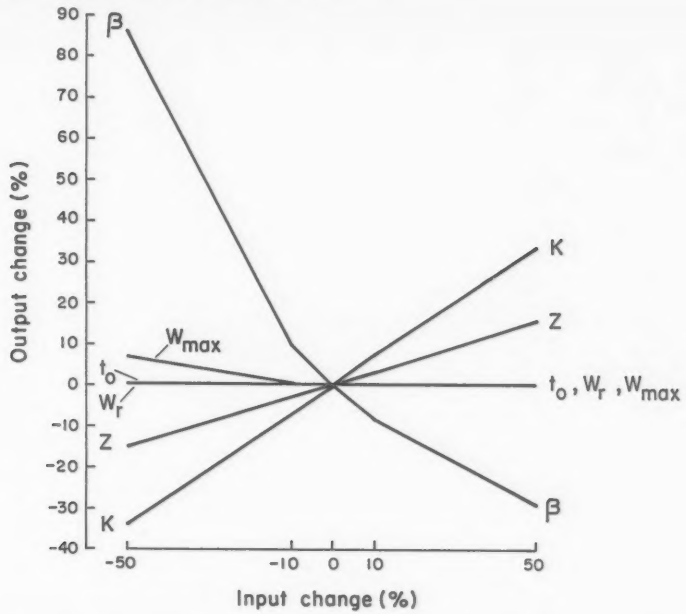

FIGURE 3.—Sensitivity analysis of Equation (22), based on parameter estimates in Table 4 for *Epinephelus guttatus*. Note strong effects of changes in β, intermediate effects of K and Z, and negligible effects of W_{max}, W_r, and t_0.

TABLE 2.—Properties and parameter values of *Epinephelus guttatus* and *Holacanthus bermudensis* relevant to the computation of their food consumption (based on data in Menzel 1958, 1960; See Table 1 and text).

Property/ parameter	*Epinephelus guttatus*	*Holacanthus bermudensis*
Asymptotic weight (g)	[1]1,880	[2]800
K (1/yr)	[1]0.24	[3]0.25
t_0 (yr)	[4]−0.2	−0.2
t_r (yr)	[5]0.35	[5]0.45
β	[6]0.136	[2]0.040
Z (1/yr)	[1]0.64	[7]0.72
t_{max} (yr)	[8]12	[8]12
food (in experiments)	fish (*Anchoa*, *Sardinella* and *Harengula*)	Algae (*Monostroma oxysperma* and *Enteromorpha satina*)

[1]From Thompson and Munro (1977); Z = 0.64 refers to an unfished stock and is thus an estimate of M.

[2]From data in Table 1 and Equation (13).

[3]Based on method in Pauly and Munro (1984) and on growth parameter estimates pertaining to members of the related family Acanthuridae, in Pauly (1978).

[4]Assumed; has little influence on results (see text and Figure 3).

[5]Corresponding to a fish of 1 g with growth parameters W_∞, K, and t_0 as given.

[6]See text and Figure 2.

[7]Based on equation (11) in Pauly (1980), with T = 28°, L_∞ = 30 cm, K = 0.25, and M = Z.

[8]Assumed; has little influence on results (see text and Figure 3).

QUANTITIES OTHER THAN Q/B ALSO ESTIMATED BY THE MODEL

In addition to estimating Q/B, the model presented above can be used to obtain other useful quantities; namely, 1) maintenance ration and related information, and 2) trophic efficiency.

Although there are differences between authors, maintenance ration is usually defined as the food used by fish to just maintain their weight at some "routine" level of activity. Usually, maintenance ration is estimated by feeding fish over a wide range of rations and determining by interpolation the ration generating neither weight gains nor losses (Jones 1976).

The model presented here allows the estimation of maintenance ration (even if fish have been fed constant rations) through extrapolation of weight-specific estimates of Q/B, such as presented in Figure 4 to the size W_∞, i.e., to the size at which, by definition, all food consumed by a fish is used for maintenance. In the case of the feeding data on *E. guttatus* analyzed here, an estimate of daily main-

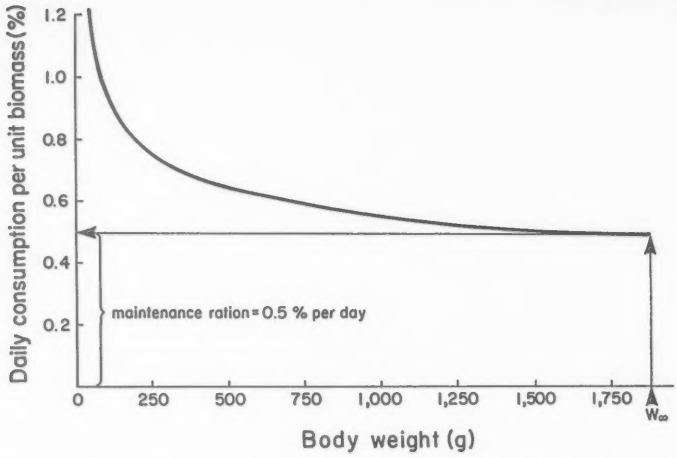

FIGURE 4.—Size-specific estimates of food consumption per unit biomass in *Epinephelus guttatus*, as obtained by integrating Equation (22) over narrow ranges of weight, then plotting the resulting Q/B estimates against the midranges of the weights. Note definition of maintenance ration as "Q/B at W_∞".

tenance ration of 0.5% body weight per day is obtained (Fig. 4), while the corresponding value for *H. bermudensis* is 1.73%.

Using the computed output of Equation (22) one can also obtain an estimate of population trophic efficiency (E_T) from

$$E_T = Z \cdot (B/Q) \qquad (25)$$

which expresses production per unit food consumed, production being expressed here as total mortality (i.e., production/biomass ratio) times biomass (Allen 1971).

For *E. guttatus*, the estimated value of trophic efficiency is $E_T = 0.23$, i.e., slightly less than one quarter of the fish food eaten by a population of *E. guttatus* is turned into production. The corresponding value for *H. bermudensis* is $E_T = 0.08$, which is low, as should be expected in an herbivore.

ACCOUNTING FOR MULTIFACTOR EFFECTS ON K_1

Experimental data allowing for the estimation of values of W_∞ and β corresponding exactly to those to be expected in nature cannot be obtained, since no experimental design can account for all the environmental factors likely to affect the food conversion of fishes in nature. Among the factors which can be experimentally accounted for are

1) ration size (Paloheimo and Dickie 1966; but see Condrey 1982),
2) type of food (see below),
3) temperature (Menzel 1958, Taylor 1958, Kinne 1960, and see below),
4) salinity (Kinne 1960).

Also, "internal states" affecting food conversion efficiency, such as the sex of the fish, previous thermal history, and stress undergone during an experiment, can be accounted for given a suitable experimental design.

One method of incorporating some of these factors into a linear form of the basic model (Equation (5)) is to extend the model into a multiple regression of the form

$$C = a - \beta \log_{10} W + b_1V_1 + b_2V_2 \ldots b_nV_n \qquad (26)$$

in which V_1, V_2, and V_n are factors which affect C ($= -\log_{10}(1 - K_1)$) after the effect of weight on C has been accounted for.

For example,

$$C = 0.363 - 0.0419W - 0.0116T + 0.0156S + 0.0488M \qquad (27)$$

is derived from the results of experiments conducted with dab (*Limanda limanda*) by Pandian (1970, figs. 5, 6)[4] in which the type of food, M (0 = herring meat, 1 = cod meat), and sex, S (0 = ♂, 1 = ♀), and the temperature, T (in °C) were reported in addition to the weight, W (in g and $\log_{10}$ units).

This model permits exact tests on the effects of each factor (Table 3), and permits adjusting parameter values (W_∞, β) so that they relate to conditions resembling those occurring in nature.

Then, W_∞ is estimated—at least in principle—from

$$W_\infty = \text{antilog}_{10}\,(1/\beta)\,(a + b_1V_1 + b_2V_2 \ldots b_nV_n). \quad (28)$$

This equation implies that there is, for every combination of V_1, V_2, ... V_n values, a corresponding value of W_∞. This is reasonable, as it confirms that W_∞ is environmentally controlled (Taylor 1958; Pauly 1981, 1984b). W_∞-values obtained through Equation (31) will generally be reliable—as was the case with the one-factor model (4)—only when a wide range of weights are included, variability is low, and the correct statistical model is used.

As a first approach toward an improved statistical model, one could conceive of a geometric mean multiple regression which, in analogy to a simple geometric mean regression, would be derived from the geometric mean of the parameters of a series of multiple regressions. This approach would involve, in the case of $n + 1$ variables (= Y, Y_1, Y_2, ... Y_n) in the following steps:

1) Compute the parameters of $n + 1$ Type I multiple regressions, where each regression (j) has another variable as dependent variable (i.e., Y, then Y_1, Y_2, ... to Y_n; see j = 1 to 5 in Table 4).

2) Solve each of the j equations for the "real" dependent variable ($Y = C$, see j = 6 to 10 in Table 4).

3) Compute the geometric mean of each partial regression coefficient from

$$b_i' = (b_{1j} \cdot b_{2j} \cdot \ldots b_{nj})^{1/n}. \quad (29)$$

4) Compute the intercept of the new Type II

[4]A table listing all values extracted from figures 5 and 6 in Pandian (1970) is included in the document mentioned in footnote 1, and will be supplied on request by me.

TABLE 3.—Details of a Type I multiple regression to quantify the effects of some factors on the food conversion efficiency of dab (*Limanda limanda*) (see text footnote 3).

Source of variation	Degrees of freedom	Sum of squares	Mean squares
Regression	4	0.0813	0.0203
Residual	57	0.0516	0.0009
Total	61	0.1329	

$F(4.57)$ 22.465 $P < 0.001$

multiple correlation = 0.7822
R^2 = 0.6119
Corrected R^2 = 0.5846
Standard error = 0.0301

Variable	Coefficient	t	SE	P
Weight	−0.041869	−3.926	0.0107	<0.001
Temp	−0.011584	−7.362	0.0016	<0.001
Sex	0.015635	1.982	0.0079	0.049
Meat	0.048840	5.301	0.0092	<0.001
Constant	0.363416	—	—	—

TABLE 4. Estimation of parameters in a "mixed" multiple regression (see also text).

j	Dependent variable	Constant ("a")	Independent variables and partial regression coefficients[1]								Remarks and R^2
1	C	= 0.363	−0.0419	W	−0.016	T	+0.0156	S	+0.0488	M	0.585
2	W	= 3.52	−5.08	C	−0.0820	T	+0.0693	S	+0.300	M	0.199
3	T	= 23.1	−2.45	W	−42.1	C	+1.07	S	+1.94	M	0.490
4	S	= −1.30	+0.151	W	+0.0780	T	+4.13	C	−0.285	M	0.035
5	M	= −2.32	+0.341	W	+0.0739	T	−0.149	S	+6.76	C	0.295
6	C	= 0.363	−0.419	W	−0.0116	T	+0.0156	S	+0.0488	M	—
7	C	= 0.693	−0.197	W	−0.0161	T	+0.0136	S	+0.0591	M	—
8	C	= 0.549	−0.0582	W	−0.0238	T	+0.0254	S	+0.0461	M	—
9	C	= −0.315	−0.0366	W	−0.0189	T	+0.242	S	+0.0690	M	not used,
10	C	= −0.345	−0.0504	W	−0.0109	T	+0.0220	S	+0.148	M	see text
mean partial regression coefficients: (for j = 6-8)			b_i = −0.0783		−0.0164		+0.0175		+0.0510		
11	0.1564 = a' − (0.0.83 · 1.738) − (0.164 · 13.32) + (0.0175 · 0.581) + (0.051 · 0.226)										
12	C	= 0.4892	−0.0783	W	−0.0164	T	+0.0175	S	+0.051	M	final result

[1]Note that body weight (W) is here expressed in $\log_{10}$ units.

multiple regression from

$$a' = \bar{Y} - (b_1'\bar{Y}_1 + b_2'\bar{Y}_2 \ldots + b_n'\bar{Y}_n) \quad (30)$$

where the $\bar{Y}_i$ are the means of the Y_i-values and b_i' the geometric mean partial regression coefficients.

This method cannot be used here without modification because in most cases the multiple regression is "mixed" (Raasch 1983), consisting of variables which can be expected to generate normally distributed residuals when used as dependent variables (here: C, W, T) as well as "dummy" or binary variables (S, M) which cannot generate normally distributed residuals when they are used as dependent variables.

As might be seen in Table 4, the use of dummy variables as "dependent" variables generates unstable interrelationships between the remaining variables, making the computation of meaningful mean partial regression coefficients impossible.

The best solution here seems to omit for the computation of the mean regression coefficient those multiple regressions which have binary variables as "dependent" variables; Table 4 illustrates this approach.

The mixed model so obtained is

$$C = 0.489 - 0.0738W - 0.0164T + 0.0175S + 0.0151M \quad (31)$$

which corresponds to the standard model

$$C' = 0.62W' - 0.90T' + 0.19S' + 0.46M' \quad (32)$$

in which the original variables C, W, T, S, and M are expressed in standard deviation units and in which the slopes (= path coefficients, see Li 1975) allow for comparing the effects of W, T, S, and M on C. These variables suggest that with regards to their impact on C,

$$T > W > M >> S. \quad (33)$$

See Li (1975) for further inferences based on path coefficients.

In the southern North Sea in late summer-early autumn, *Limanda limanda* experiences temperatures usually ranging between 10° and 20°C (Lee 1972). Solving Equation (31) for T = 18°C, the highest temperature in Pandian's experiments (i.e., assuming the higher late summer-early autumn temperatures limit W_∞) leads to estimates of W_∞ = 500 g for the females and 298 g for the males, compared with the values of 756 and 149 g obtained by Lee (1972) on the basis of growth studies.

Estimating values of β that are wholly compatible with the latter estimates of W_∞ is straightforward, however, since it consists of solving Equation (31) for T = 18°C, M = 0, and the appropriate value of S, based on the equation

$$\beta = 1/\log W_{(\infty)}\,(a + b_1'V_1 + b_2'V_2 \ldots b_n'V_n) \quad (34)$$

In the present case, this leads to β values of 0.073 and 0.089 for females and male dab, respectively. The "average" relationship (if such exists) between food conversion efficiency and body weight in female dab fed herring meat is thus

$$K_1 = 1 - (W/756)^{0.073} \quad (35)$$

while for males it is

$$K_1 = 1 - (W/149)^{0.089} \quad (36)$$

with both values of β within the 95% confidence interval of the first estimate of β (in Equation (27), see Table 3).

DISCUSSION

The model presented here for the computation of Q/B is not meant to compete against the more sophisticated models whose authors were cited above. Rather, it was presented as a mean of linking up the results of feeding experiments with elements of the theory of fishing such that inferences can be made on the food consumption of fish populations which 1) do not invoke untenable assumptions, 2) make maximum use of available data, and 3) do not require extensive field sampling.

A distinct feature of the method is that it does not require sequential slaughtering of fish for the estimation of their stomach evacuation rate, nor field sampling of fish stomachs, which may be of relevance when certain valuable fishes are considered (e.g., coral reef fishes in underwater natural parks).

Several colleagues who reviewed a draft version of this paper suggested that Equation (4) should incorporate an upper limit for K_1 smaller than unity. This model would have the form

$$K_1 = K_{1\max} - (W/W_\infty)^{\beta_m} \quad (37)$$

with parameters W_∞ and β_m identical and analogous respectively to those in Equation (4) and a value of

K_{1max} to be estimated independently prior to fitting Equation (37) to data.

Data do exist which justify setting the upper limit of K_1 at or near unity. They pertain to fish embryos, whose gross conversion efficiency can be defined by

$$K_1 = \frac{W_h}{W_e - W_y} \quad (38)$$

where W_h is the larval weight at hatching, W_e the egg weight, and W_y is the weight of the yolk sac at hatching. Values of K_1 as high as 0.93 have been reported using this approach (From and Rasmussen 1984), extending further toward unity the range of K_1 values reported by earlier authors, e.g., 0.85 in *Solea solea* (Flüchter and Pandian 1968), 0.79 in *Sardinops caerulea* (Lasker 1962), and 0.74 in *Clupea harengus* (Blaxter and Hempel 1966).

Thus, for a wet weight of 0.5 mg corresponding to a spherical egg of 1 mm diameter, one obtains, using Equation (14) for *E. guttatus*, a value of $K_1 = 0.87$ which is within the range of K_1 values given above. This example is not meant to suggest that K_1 values pertaining to large fish should be used in combination with the model presented here to "estimate" K_1 in eggs or larvae. Rather, it is meant to illustrate the contention that, of the possible choices of an upper bound for K_1 in Equation (4), the one selected here has the feature of making the model robust, particularly with respect to high values of K_1 and extrapolations toward low values of W.

Apart from β, the key elements of the model (isometric von Bertalanffy growth, constant exponential decay, steady-state population) are all parts of other, widely used models. Thus, whether estimates of Q/B obtained by this model are considered "realistic" or not will depend almost entirely on the value of β used for the computation.

There are several ways of reducing the uncertainty associated with β. The following may need special consideration:

1) Feeding experiments used to estimate β could be run so as to mimic as closely as possible the crucial properties of the habitat in which the population occurs whose Q/B value is estimated, inclusive of seasonally oscillating factors.

2) Further research and study should lead to the identification of anatomical, physiological, and ecological properties of fish correlating with their most common value of β.

3) An additional parameter could be added to account for fish reproduction, which is not explicitly considered in Equation (22).

Little needs to be said about item 1 which should be obvious since (except in the context of aquaculture) feeding and growth experiments are conducted in order to draw inferences on wild populations. With regards to item 2, it suffices to mention that relative gill area (= gill surface area/body weight), which appears to a large extent to control food conversion efficiency (Pauly 1981, 1984b), should be a prime candidate for correlational studies. Item 3 could cause Q/B values obtained by the model presented here to substantially underestimate actual food consumption, were it not for three circumstances which produce opposite tendencies:

a) The assumption that the energy needed by fish to develop gonads is taken from the energy otherwise available for growth may not apply (Iles 1974; Pauly 1984b). Rather, the reduction of activity occurring in some maturing fish may more than compensate for the energy cost of gonad development (Koch and Wieser 1983).

b) Growth parameters are usually computed using size data from fish whose gonads have not been removed, thus accounting for at least a fraction of the food converted into gonad tissue. When the value of Z used in the model is high, this fraction will be large because the contribution of the older fish to the overall estimate of Q/B will be small.

c) Experimental fish are usually stressed and therefore have lower conversion efficiencies than fish in nature, even though they may spend little energy on food capture (see Edwards et al. 1971). This effect leads to low values of β and hence high estimates of Q/B.

Because of these factors, the values of Q/B obtained by the method proposed here may lack a downward bias.

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LITERATURE CITED

ALLEN, K. R.
1971. Relation between production and biomass. J. Fish.

Res. Board Can. 28:1573-1581.

ANDERSEN, K. P.
1982. An interpretation of the stomach contents of fish in relation to prey abundance. Dana 2:1-50.

ARMSTRONG, D. W., J. R. G. HISLOP, A. P. ROBB, AND M. A. BROWN.
1983. A preliminary report on the analysis of whiting stomachs collected during the 1981 North Sea Stomach Sampling Project. ICES. Doc. C.M. 1983/G:59.

BARDACH, J. E., J. H. RYTHER, AND W. O. MCLARNEY.
1972. Aquaculture: the farming and husbandry of freshwater and marine organisms. Wiley-Inter-Science, N.Y., 868 p.

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol. 10:181-213.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish Food (G.B.) Ser. II, Vol. 19, 533 p.

BLAXTER, J. H. S., AND G. HEMPEL.
1966. Utilization of yolk by herring larvae. J. Mar. Biol. Assoc. U.K. 46:219-234.

CONDREY, R. E.
1982. Ingestion-limited growth of aquatic animals: the case for Blackman kinetics. Can. J. Fish. Aquat. Sci. 39:1585-1595.

DAAN, N.
1973. A quantitative analysis of the food intake of North Sea cod, (*Gadus morhua*). Neth. J. Sea Res. 6:479-517.
1983. Analysis of the cod data collected during the 1981 stomach sampling project. ICES Doc. C.M. 1983/G:61.

EDWARDS, R. R. C., J. H. S. BLAXTER, U. K. GOPALAN, C. V. MATHEW, AND D. M. FINLAYSON.
1971. Feeding, metabolism, and growth of tropical flatfish. J. Exp. Mar. Biol. Ecol. 6:279-300.

FLÜCHTER, J., AND T. J. PANDIAN.
1968. Rate and efficiency of yolk utilization in developing eggs of the sole *Solea solea*. Helgol. Wiss. Meeresunters. 18:53-60.

FROM, J., AND G. RASMUSSEN.
1984. A growth model, gastric evacuation and body composition in rainbow trout, *Salmo gairdneri* Richardson 1836. Dana 3:61-139.

GULLAND, J. A.
1983. Fish stock assessment: a manual of basic methods. John Wiley and Sons, N.Y., 223 p.

ILES, T. D.
1974. The tactics and strategy of growth in fishes. *In* F. R. Harden-Jones (editor), Sea fisheries research, p. 331-345. Elek Sci. Books, Ltd., Lond., 511 p.

IVLEV, V. S.
1939. Balance of energy in carps. [In Russ.] Zool. Zh. 18: 303-318.
1966. The biological productivity of waters. J. Fish. Res. Board Can. 23(11):1727-1759. W. E. Ricker (transl.).

JONES, R.
1976. Growth of fishes. *In* D. H. Cushing and J. J. Walsh (editors), The ecology of the seas, p. 251-279. Blackwell Scientific Publications, Oxford.

KINNE, O.
1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zoöl. 33:288-317.

KOCH, F., AND W. WIESER.
1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? J. Exp. Biol. 107:141-146.

LASKER, R.
1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine *Sardinops caerulea* (Girard). J. Fish. Res. Board Can. 19:867-875.

LEE, C. K. G.
1972. The biology and population dynamics of the common dab *Limanda limanda* (L.) in the North Sea. Ph.D. Thesis, Univ. East Anglia.

LI, C. C.
1975. Path analysis: a primer. The Boxwood Press, Pacific Grove, CA, 347 p.

MAJKOWSKI, J.
1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. *In* D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries, p. 149-165. ICLARM Conf. Proc. 9, 360 p.

MAJKOWSKI, J., AND W. S. HEARNS.
1984. Comparison of three methods for estimating the food intake of a fish. Can. J. Fish. Aquat. Sci. 41:212-215.

MENZEL, D. W.
1958. Utilization of algae for growth by the Angelfish *Holacanthus bermudensis*. J. Cons. Int. Explor. Mer 24:308-313.
1960. Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. J. Cons. Int. Explor. Mer 25:216-222.

PALOHEIMO, J. E., AND L. M. DICKIE.
1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23:1209-1248.

PANDIAN, T. J.
1967. Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol. (Berl.) 1:16-32.
1970. Intake and conversion of food in the fish *Limanda limanda* exposed to different temperatures. Mar. Biol. (Berl.) 5:1-17.

PAULY, D.
1978. A preliminary compilation of fish length growth parameters. Ber. Inst. f. Meeresk., Univ. Kiel No. 55, 200 p.
1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39:175-192.
1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28:251-282.
1982. Studying single-species dynamics in a tropical multispecies context. *In* D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries, p. 33-70. ICLARM Conf. Proc. 9, Manila, 360 p.
1984a. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8, Manila, 325 p.
1984b. A mechanism for the juvenile-to-adult transition in fishes. J. Cons. Int. Explor. Mer 41:280-284.

PAULY, D., AND J. L. MUNRO.
1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1):21.

PENNINGTON, M.
1984. Estimating the average food consumption by fish in the field from the stomach contents data. I.C.E.S., Doc. C.M. 1984/H:28.

POLOVINA, J. J.
1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1-11.

RANDALL, J. E.
1968. Caribbean Reef Fishes. T.F.H. Publications, Neptune City, NJ, 318 p.
RASCH, D. (editor)
1983. Biometrie: Einführung in die Biostatistik. VEB Dtsch. Landwirtschaftsverlag, Berl., 276 p.
RICE, J. A., J. E. BRECK, S. M. BARTELL, AND J. F. KITCHELL.
1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fishes 9:263-275.
RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
SPRUGEL, D. G.
1983. Correcting for bias in log-transformed allometric equations. Ecology 64:209-210.
STEWART, D. J., D. WEININGER, D. V. ROTTIERS, AND T. A. EDSALL.
1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40:681-698.
TAYLOR, C. C.
1958. Cod growth and temperature. J. Cons. Int. Explor. Mer 23:366-370.
THOMPSON, R., AND J. L. MUNRO.
1977. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). J. Fish. Biol. 12: 115-146.
URSIN, E.
1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board Can. 24: 2355-2453.

APPENDIX

List of symbols used in model development and illustration

A_1-A_4 terms used in computation of biomass per recruit (Equation (21))

a - multiplicative term in equation linking K_1 and body weight (Equation (3))

- intercept of a Type I (multiple) linear regression

a' - intercept of a Type II (multiple) linear regression

b - slope of a Type I linear regression

- exponent in equation linking K_1 and body weight

b_c - slope of a Type I multiple linear regression

b' - slope of a Type II linear regression

b_i' - slope of a Type II multiple linear regression

B - biomass (under equilibrium condition)

β - exponent in model linking K_1 and body weight (Equation (4))

β_m - similar to β, but estimated jointly with $K_{1\max}$ (Equation (37))

C - $(-\log_{10}(1 - K_1))$

C' - same as C, but expressed in standard deviation units

dq/dt - rate of food consumption

dw/dt - rate of growth in weight

E_T - trophic efficiency, i.e., production by population/food consumption by population

i - counter for number of variables in a multiple regression

j - counter for number of multiple regressions

K - constant in VBGF

K_1 - gross conversion efficienty (Equation (1))

$K_{1\max}$ - hypothetical upper limit for K_1 (with $K_{1\max} < 1$) (Equation (37))

M - instantaneous rate of natural mortality

- a dummy variable expressing food type (Equation (27))

M' - a dummy variable expressing food type in standard deviation units

n - number of partial regression coefficient used in computing a given value of b_i'

N - number of fish in population (Equation (19))

Q - food consumption of a population (per unit time)

Q/B - food consumption per unit biomass of an age-structured animal population

Q_c - cumulative food consumed by a single fish between ages t_r *and* $t_{\max}$ (Equation (22))

R - number of recruits (Equation (19))

r - product moment correlation coefficient

S - a dummy variable expressing sex

S' - a dummy variable expressing sex in standard deviation units

t - age

t_c - mean age at first capture (in an exploited stock)

t_0 - α parameter of the VBGF expressing the theoretical age at size zero

$t_{\max}$ - maximum age considered (= longevity)

t_r - mean age at recruitment to the part of the population considered when computing Q/B

T - temperature in °C

T' - temperature in °C, expressed in standard deviation units (Equation (32))

V_i - any variable beyond W which affects K_1

VBGF - the von Bertalanffy growth function

W - body weight (in log units in some cases)

W' - body weight (in $\log_{10}$ units), expressed in standard deviation units

W_c - weight of a fish egg

W_h - weight of a fish at hatching (yolk sac excluded)

$W_{\max}$ - body weight corresponding to $t_{\max}$

W_r - body weight corresponding to t_r

W_t - mean weight at age t

W_y - yolk sac weight in a newly hatched fish

W_∞ - asymptotic weight in the VBGF or in new model (Equation (4))

$W_{(\infty)}$ - an estimate of asymptotic weight obtained indirectly (i.e., from data of a type different than those in model using value of $W_{(\infty)}$)

Y_i - any variable included in a multiple regression

Z - instantaneous rate of mortality (= P/B ratio)

REPRODUCTIVE BIOLOGY OF KING MACKEREL, *SCOMBEROMORUS CAVALLA*, FROM THE SOUTHEASTERN UNITED STATES

JOHN H. FINUCANE, L. ALAN COLLINS, HAROLD A. BRUSHER, AND CARL H. SALOMAN[1]

ABSTRACT

The reproductive biology of king mackerel, *Scomberomorus cavalla*, was studied from specimens collected off Texas, Louisiana, and northwest Florida in the Gulf of Mexico and off North and South Carolina in the Atlantic Ocean. Gonads were examined from 1,163 females and 595 males obtained in 1977-78. Spawning was prolonged. Most king mackerel were reproductively active from May through September. A few fish were in spawning condition as early as April and as late as October. All females were mature at 850-899 mm fork length (FL). Estimates of fecundity ranged from about 69,000 to 12,207,000 eggs for fish from 446 to 1,489 mm FL, 618 to 25,610 g total weight (TW), and 1 to 13 years of age. Fecundity (F) was usually significantly correlated with FL, TW, and age in each area but TW was the best predictor of fecundity in all areas combined ($F = 1.854 \times 10^1 (TW)^{1.361}$) with $r^2 = 0.856$.

King mackerel, *Scomberomorus cavalla*, is one of the most valuable commercial and recreational fish in the Gulf of Mexico and south Atlantic. It is an epipelagic, neritic species that occurs in the western Atlantic Ocean from Massachusetts to Rio de Janeiro, Brazil (Collette and Russo 1979, 1984). Most of the king mackerel caught off the southeastern United States are landed in Florida (Manooch 1979) where it is an important component of charter boat catches (Moe 1963; Brusher et al. 1978). Commercial landings in Florida during 1983 totaled 2,017 t and the estimated recreational catch from the Gulf of Mexico was 1,090,000 fish in 1984 (U.S. Department of Commerce 1985a, b).

Although much has been written on king mackerel, little is known of its reproductive biology (Manooch et al. 1978). Ovarian histology and size-at-maturity has been described by Alves and Tome (1967) for fish from Brazil and by Beaumariage (1973) for fish from Florida. Maturation based on blood hormone levels from fish off northwest Florida was reported by MacGregor et al. (1981). Spawning times and areas have been inferred from ichthyoplankton collections of king mackerel larvae (Dwinell and Futch 1973; Finucane and Collins 1977; Houde et al. 1978[2]; McEachran et al. 1980). The only fecundity estimates in the literature were made by Ivo (1974) for fish from Brazil.

The purpose of our study was to provide additional information on king mackerel reproductive biology by determining spawning season, length-at-maturity, and fecundity from four areas off the southeastern coast of the United States. This information will be useful in the management of king mackerel since the measure of reproductive potential is a basic element of productivity and stock dynamics (Baglin 1982).

METHODS

King mackerel were sampled from commercial and recreational catches in four separate areas along the coast of the southeastern United States during 1977 and 1978 (Fig. 1). These areas were I, the northwestern Gulf of Mexico off the central and south coasts of Texas; II, the northcentral Gulf off Louisiana and Mississippi; III, the northeastern Gulf off northwest Florida; and IV, the western Atlantic Ocean off South and North Carolina.

Procedures for processing gonads, weighing, and measuring fish followed the methods of Finucane and Collins (1984). If no total weight had been recorded for a fish, we estimated TW by using the formula $TW = 1.4959 \times 10^{-5} (FL)^{2.89284}$ (TW = total weight in grams; FL = fork length in millimeters). This formula (Ricker 1975) was derived

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[2]Houde, E. D., J. C. Leak, C. E. Dowd, S. A. Berkely, and W. J. Richards. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Part I: Executive summary, abstract, text reference. Unpubl. manuscr., 119 p. Draft Final Report to Bureau of Land Management, Contract AA550-CT7-28. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.

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FIGURE 1.—Sampling areas for king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico and Atlantic Ocean during 1977-78.

from a length-weight regression (r = 0.996; n = 186) of king mackerel data from all areas.

Egg size distributions within the ovary were statistically compared to ensure that subsamples taken for studies of maturation and fecundity were representative (Yuen 1955; Otsu and Uchida 1959). Both ovarian lobes were divided into three sections (anterior, middle, and posterior) of about equal length. At a selected point along each of these sections, a 2-4 mm thick cross section was cut and removed. A wedged-shaped portion was then taken from each of the three cross sections and divided into three zones: inner, middle, and outer. A sample of 150 yolked eggs from each of the zones was examined with a microscope and all eggs were measured to the nearest 0.02 mm at 500× on whatever axis the egg happened to be located in respect to an ocular micrometer scale (Clark 1934). A chi-square test of independence (Steel and Torrie 1960) was used to test for significant differences in mean egg diameters (EDs) among the sections, zones, and zones within a section in each lobe.

Each wedge-shaped sample of eggs was placed in a dish with 10% Formalin[3] and the eggs were then teased apart. Samples containing only unyolked eggs (≤0.20 mm ED) were considered to be from immature fish and only 100 eggs from these samples were measured. Samples with yolked eggs (≥0.20 mm ED) were considered to be from mature fish and 300 eggs were measured.

Seasonal maturation was determined by plotting monthly mean EDs of the most advanced eggs found in each ovary and by gonadosomatic indices (GSI = the percentage of TW represented by gonad weight). The range and 95% confidence interval of the monthly mean GSIs were also plotted. To compare the variation of GSIs, we calculated the coefficient of variation for each month. We estimated the length at which the fish first matured by computing mean GSIs for fish in each 50 mm interval and used the length at which the greatest increase in mean GSIs between consecutive FL intervals occurred. For this analysis we only used data that were collected during the fish's most sexually active months as indicated by the highest values of mean EDs and GSIs. An additional estimate was made for females by assigning immature or mature status to each fish according to egg stage and then calculating the percentage of mature fish by FL intervals.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Fecundity estimates were based on the number of yolked eggs ≥0.20 mm in diameter in the most mature ovaries. Similar methods were discussed by Hunter and Goldberg (1980) and used by Morse (1980). A diameter of 0.20 mm was used to separate immature and mature eggs, because it was at this size that yolk first appeared. A gravimetric method was used for fecundity and followed the procedures of Finucane and Collins (1984). Ages of fish were determined from otoliths (Johnson et al. 1983). Analysis of covariance was used to test for differences in fecundity by year and area. Regression and correlation were used to examine the linear and curvilinear relationships between fecundity and fork length, total weight, and age.

RESULTS

Gonads from 1,165 female and 593 male king mackerel were examined. Fish ranged in FL from 351 to 1,554 mm, in TW from 658 to 31,780 g, and in age from 1 to 13 yr. Temporal coverage varied from 3 mo in area I to 12 mo in area II. Number and percentage composition of fish by area were area I, 85 and 4.8%; area II, 646 and 36.7%; area III, 768 and 43.7%; and area IV, 259 and 14.7%.

Analysis of the egg size distribution indicated that there were significant differences ($\alpha = 0.05$) in ED between the inner, middle, and outer zones within ovarian sections; there were no differences between sections. Therefore, we took a wedge-shaped sample (representing the three cross-sectional zones) from the middle of the right or left ovary as representative of the entire ovary for ED analysis. King mackerel ovaries were grouped into five reproductive stages based on ED. Stage I (immature ovaries) contained eggs ≤0.06 mm. Eggs in stage II (resting ovaries) ranged from 0.07 to 0.20 mm. Stage III (maturing) and stage IV (mature) ovaries contained eggs 0.21-0.50 mm and 0.51-0.71 mm, respectively. Stage V eggs measured 0.71-1.20 mm and indicated ripe ovaries.

The seasonal progression of mean GSIs and EDs indicated that king mackerel have a prolonged spawning season that varied between areas (Figs. 2-5). Peak spawning months occurred from May through September as observed in 14 ripe females from areas I, II, and IV. A few fish were in spawning condition as early as April and as late as October. In area I, GSIs and EDs peaked in July and August for both sexes. Area II fish had the highest GSIs and EDs for both sexes during May. In area III, GSIs for both sexes were greatest during June

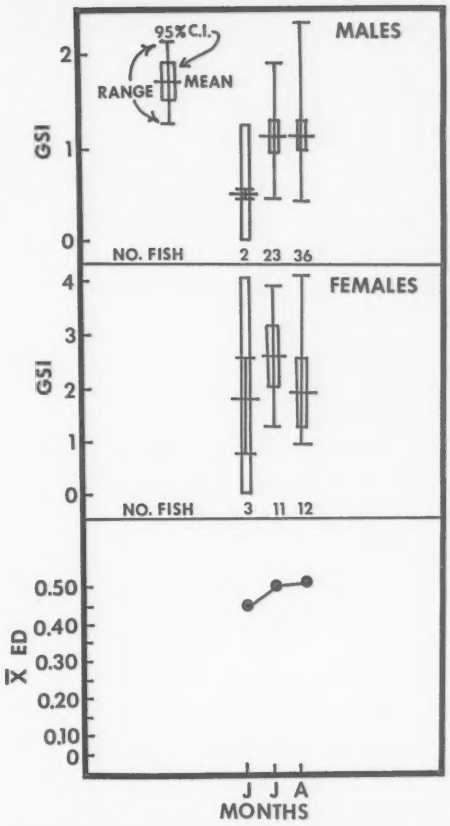

FIGURE 2.—Seasonal maturation cycle of male and female king mackerel from area I (Texas) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

while EDs peaked in August. Area IV fish had the highest female GSIs and EDs during July.

Serial spawning was suggested by several lines of evidence. Distribution of EDs was multimodal during spawning months. The highest coefficient of variation for GSIs occurred during the spawning months, suggesting that eggs were maturing and released serially throughout the spawning season (Table 1).

The size at maturation of king mackerel also varied between areas. Maturity was based on the number and percentage of fish with stage III-stage V ova for each 50 mm FL interval. Length intervals in which at least 50% of the females were mature for areas I-IV, respectively, were 450-499 mm, 600-649 mm, 600-649 mm, and 650-699 mm

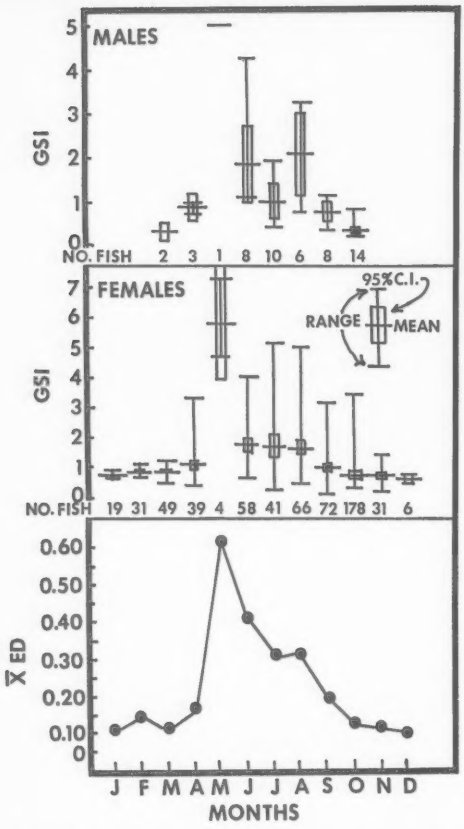

FIGURE 3.—Seasonal maturation cycle of male and female king mackerel from area II (Louisiana and Mississippi) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

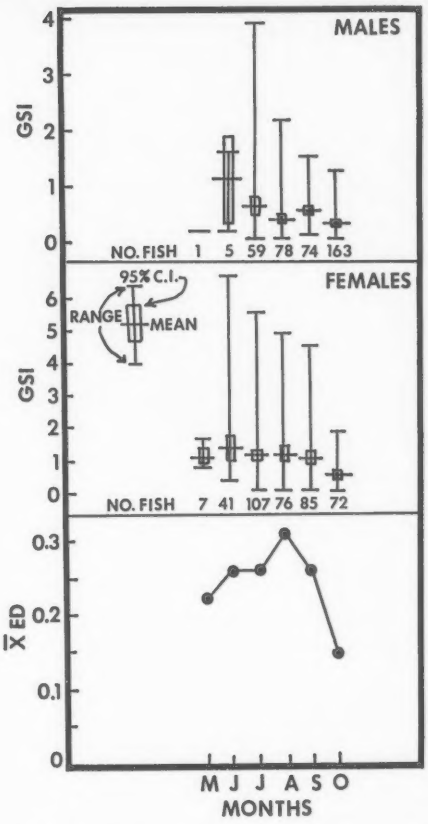

FIGURE 4.—Seasonal maturation cycle of male and female king mackerel from area III (northwest Florida) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

TABLE 1.—Coefficient of variation for monthly GSIs of female (F) and male (M) king mackerel in each area.

	Area I		Area II		Area III		Area IV	
Month	F	M	F	M	F	M	F	M
January	—	—	12.7	—	—	—	—	—
February	—	—	12.5	—	—	—	—	—
March	—	—	18.0	7.1	—	—	—	—
April	—	—	43.6	15.3	—	—	—	—
May	—	—	20.4	[1]	28.2	—	56.3	52.9
June	51.7	16.0	55.0	57.1	96.9	56.4	39.1	—
July	33.6	35.4	77.3	58.2	95.5	104.8	36.2	[1]
August	54.2	38.9	66.2	43.4	95.5	75.7	44.4	2.5
September	—	—	56.7	38.7	85.9	51.9	64.9	61.5
October	—	—	36.8	48.4	62.7	51.6	41.7	54.5
November	—	—	32.8	—	—	—	—	—
December	—	—	20.0	—	—	—	—	—

[1] $n = 1$

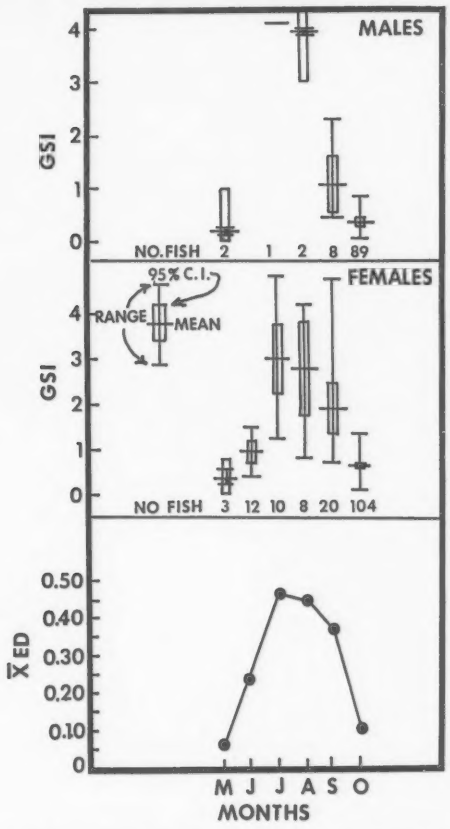

FIGURE 5.—Seasonal maturation cycle of male and female king mackerel from area IV (North and South Carolina) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

(Table 2). All females were mature at 850-899 mm. Another maturation pattern was noted when the midpoints of fork length intervals were plotted against mean GSIs for each area (Fig. 6). The size interval where greatest increases in GSIs occurred were 650-699 mm (area I), 700-749 mm (area II), 450-499 mm (area III), and 650-699 (area IV).

Fecundity ranged from 69,000 to 12,207,000 eggs in 65 king mackerel from all areas. Fish ranged in FL from 446 to 1,489 mm, in TW from 681 to 25,610 g, and in age from 1 to 13 yr (Table 3). Analysis of covariance with TW as the covariate showed no significant differences ($\alpha = 0.05$) in fecundity between years or among areas. The best predictor of fecundity based on regression and correlation analysis was TW for areas II, IV, and all areas combined and FL for areas I and III (Table 4). Log transformed linear models were better predictors of fecundity than nontransformed models in all areas but area IV.

DISCUSSION

Our results on the seasonal maturation and protracted spawning season of king mackerel agree closely with other studies. In waters off Florida, Beaumariage (1973) found late-maturing (stages III and IV) eggs in king mackerel from May through October. In the northeastern Gulf of Mexico (area III), Dwinell and Futch (1973) caught king mackerel larvae during the same time interval and MacGregor et al. (1981) reported early- or late-maturing ovaries from August through October. In the northwestern Gulf of Mexico off Texas (area I), Finucane and Collins (1977) and McEachran et al. (1980) noted catches of larvae from May through August, and April through October, respectively. In the area off Cape Fear, NC, to Cape Canaveral, FL, Powles[4] collected king mackerel larvae from May through September.

Length at maturation was difficult to determine because the sample size of small fish (<600 mm) was limited in all areas except area III (northwest Florida). Using only fish from this area, maturity first occurred about 450-499 mm and 50% of the fish were mature at about 550-599 mm. These estimates of maturity agreed with some of the other studies. Female king mackerel first reached sexual maturity at 630 mm and 4 yr of age (Gesteira and Mesquita 1976) or at 586 mm (Alves and Tome 1967) off Brazil. Another study on Brazilian fish, however, noted that females were first mature at 770 mm and 5-6 yr of age (Ivo 1972). In Florida waters, Beaumariage (1973) estimated that females 3 yr or younger were immature and probably had not spawned. He believed that the first major spawning by females and males occurred at 880 and 770 mm SL, respectively. Some of his 1-yr-old females contained stage IV eggs that had been aborted or reabsorbed since he did not find ripe (stage V) eggs until the fish were 4 yr old. His standard length for king mackerel from Florida at age 1 was 610 mm (651 mm FL), which was higher than our estimate of length at first maturity.

[4]Powles, H. W. Abundance and distribution of king mackerel, (*Scomberomorus cavalla*) and Spanish mackerel (*S. maculatus*) larvae of the southeast United States. Unpubl. manuscr. Gouvernement du Canada, Peches et Oceans, Division des Sciences halieutiques, C. P. 15500, Quebec, Canada G1K 7Y7.

TABLE 2.—Total sample number and percentage of mature (Stages III-V) king mackerel females collected during the peak maturation season in each area.[1]

	Area I (Texas)		Area II (Louisiana, Mississippi)		Area III (Northwest Florida)		Area IV (North and South Carolina)	
Fork length	No.	Mature (%)	No.	Mature (%)	No.	Mature (%)	No.	Mature (%)
300-349	0	—	0	—	0	—	0	—
350-399	1	0.0	0	—	1	0.0	0	—
400-449	0	—	0	—	2	0.0	0	—
450-499	1	100.0	0	—	3	33.3	0	—
500-549	0	—	0	—	16	6.3	0	—
550-599	0	—	0	—	28	46.4	0	—
600-649	2	100.0	2	100.0	31	71.0	1	0.0
650-699	0	—	0	—	31	71.0	4	75.0
700-749	4	100.0	1	100.0	35	80.0	2	100.0
750-799	8	100.0	0	—	29	62.1	5	100.0
800-849	6	100.0	0	—	41	75.6	4	100.0
850-899	2	100.0	5	100.0	29	100.0	11	100.0
900-949	2	100.0	6	100.0	21	100.0	8	100.0
950-999	0	—	22	100.0	19	100.0	7	100.0
1,000-1,049	0	—	19	100.0	13	100.0	3	100.0
1,050-1,099	0	—	18	100.0	4	100.0	3	100.0
1,100-1,149	0	—	18	100.0	6	100.0	1	100.0
1,150-1,199	0	—	13	100.0	4	100.0	1	100.0
1,200-1,249	0	—	18	100.0	2	100.0	0	—
1,250-1,299	0	—	14	100.0	1	100.0	0	—
1,300-1,349	0	—	17	100.0	0	—	0	—
1,350-1,399	0	—	11	100.0	0	—	0	—
1,400-1,449	0	—	3	100.0	0	—	0	—
1,450-1,499	0	—	2	100.0	0	—	0	—
Total	26		169		316		50	

[1]Area I, June-August; Area II, May-August; Area III, May-September; and Area IV, June-September.

Factors influencing the maturation cycle of king mackerel are not well known. Presumably, photoperiod and water temperature are important for spawning, egg, and larval development. Beaumariage (1973) indicated that seasonal changes in photoperiod influenced the spawning of king mackerel while McEachran et al. (1980) noted that larvae were more abundant at temperatures from 20.2° to 29.8°C and salinities from 28.2 to 34.4‰. A study by MacGregor et al. (1981) also showed that the levels of serum androgens and estrogens may be indicators of maturation in king mackerel.

Our inferences on spawning peaks and activity of king mackerel, as determined by largest mean EDs, usually coincided with those of other studies. Our largest mean ED of 0.61 mm agrees with the 0.60 mm reported by Alves and Tome (1967). In contrast, the largest mean ED of 0.33 mm shown by Beaumariage (1973) suggests that most of his fish were not ready to spawn. Our largest mean egg sizes from northwest Florida fish were similar to those reported by Beaumariage (1973) and probably indicates that spawning activity off the west coast of Florida is not extensive. Peak spawning months by area in this study were area I, August; area II, May; area III, August; and area IV, July. In the northwestern and northeastern gulf, (our areas I and III) the highest catches of larval king mackerel occurred during September (Dwinell and Futch 1973; McEachran et al. 1980). Houde et al. (fn. 2) stated that because of their rare catches of larvae, king mackerel does not appear to spawn frequently in the eastern gulf.

The reproductive cycle of king mackerel off the coast of Brazil is probably similar to that of this species from American waters. Ivo (1972) noted that spawning occurred throughout the year off the state of Ceara which is south of the Equator. Other studies indicate that they begin to spawn from October through December (Menezes 1969) with peaks in November and March (Gesteria and Mesquita 1976). Since the seasons are reversed in this area, they would correspond to our spring and late summer spawning peaks for king mackerel.

We were unable to determine the number of times individual king mackerel spawn during the year from the data. Beaumariage (1973) concluded that king mackerel were multiple spawners, based on their extended spawning season and presence of several modal groups of yolked eggs. Morse (1980) reported that individual Atlantic mackerel, *Scomber*

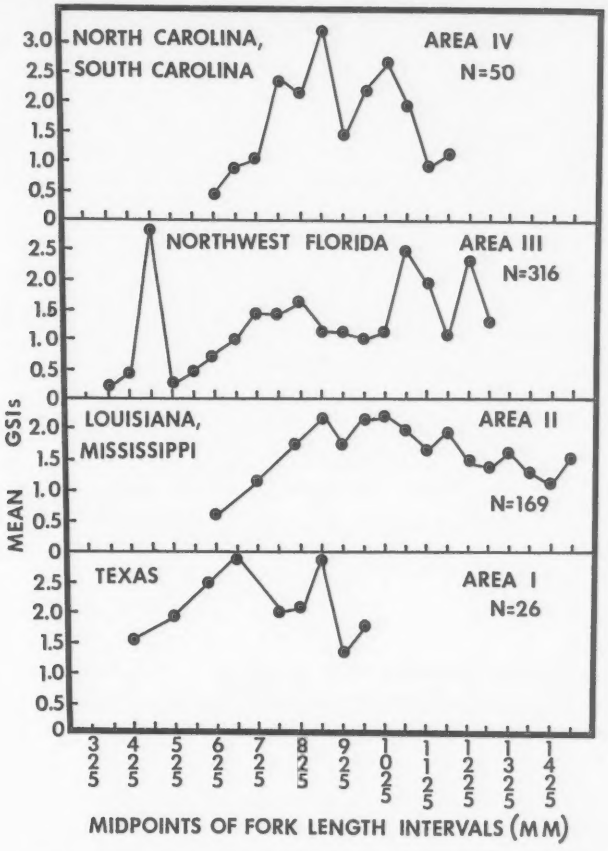

FIGURE 6.—Mean GSI plotted by midpoint of fork length interval for female king mackerel in each area.

scombrus, are capable of spawning six batches of eggs during the spawning season. Documentation of spawning frequency and numbers of eggs produced will require that king mackerel be held in captivity.

Major spawning areas for king mackerel could not be determined during this study because of the scarcity of ripe fish. Gonad maturation data suggest that spawning occurs throughout the sampling areas but the magnitude of spawning and extent of spawning areas are unknown. Ichthyoplankton surveys conducted by Wollam (1970), Houde et al. (fn. 2), and McEachran et al. (1980) have revealed general spawning locations of king mackerel by the occurrence of small larvae (<3 mm SL). These studies indicate that spawning probably occurs over the continental shelf of the northwestern and northeastern Gulf of Mexico. Most small larvae collected by McEachran et al. (1980) were captured over the middle and outer continental shelf in water depths of 35-130 m off the Texas coast.

No comparative fecundity data were available from the southeastern U.S.; however, Ivo (1974) determined fecundity for 39 fish from Brazilian waters. He found great variation in fecundity for fish with the same fork length.

The fact that disjunct spawning appears to occur off the Carolinas and in the northcentral and western Gulf of Mexico from spring through fall may suggest separate stocks of king mackerel in these areas.

TABLE 3.—Summary of data on king mackerel for which fecundity was estimated, 1977-78.

Date	Fork length (mm)	Gonad weight (g)	Total weight (g)	Gonad index (×100)	Age	Fecundity (estimated)
Area I (Texas)						
8/26/78	500	18.16	900	2.02	2	185,608
7/8/78	650	55.66	2,270	2.45	—	985,340
7/26/78	750	76.09	3,042	2.50	4	1,082,301
8/26/78	760	35.23	3,166	1.11	—	466,252
7/8/78	770	92.87	3,405	2.73	2	1,194,283
7/8/78	900	142.53	4,086	3.49	4	2,009,870
7/8/78	810	135.50	4,313	3.14	—	1,435,752
7/8/78	835	82.96	4,540	1.83	4	1,380,342
7/8/78	860	176.00	4,994	3.52	5	2,753,638
7/8/78	870	130.19	4,994	2.61	5	2,236,664
8/7/78	895	212.86	5,448	3.91	6	2,309,622
—	—	239.41	4,183	—	3	4,183,921
Area II (Louisiana)						
6/24/78	446	8.43	681	1.24	—	69,264
6/23/77	635	13.45	1,930	0.70	1	182,863
6/20/77	710	26.92	2,500	1.08	2	2,570,133
9/13/77	852	96.36	4,380	2.20	4	1,179,625
7/13/78	895	158.51	5,130	3.09	4	2,079,204
8/15/77	951	239.09	6,221	3.84	—	4,448,492
5/20/78	972	451.68	7,310	6.18	6	6,319,134
5/20/78	994	577.18	11,120	5.19	6	5,890,631
7/7/78	1,025	325.56	9,000	3.62	6	4,686,248
8/7/78	1,037	417.00	8,325	5.01	6	6,437,542
6/23/78	1,055	314.33	8,626	3.64	11	4,686,598
9/3/77	1,086	303.52	9,750	3.11	—	5,401,961
6/25/78	1,109	247.66	9,534	2.60	—	2,771,744
6/25/78	1,149	401.59	10,896	3.69	9	4,268,537
6/16/78	1,178	478.74	13,286	3.60	6	8,899,756
7/10/78	1,194	447.88	9,045	4.95	10	6,010,133
4/29/78	1,220	498.52	15,150	3.29	9	7,315,781
5/20/78	1,229	698.36	14,070	4.96	6	10,116,890
6/17/78	1,265	611.04	15,095	4.05	9	9,209,082
6/17/78	1,291	468.64	15,890	2.95	10	7,487,826
8/10/77	1,312	583.79	17,120	3.41	—	6,689,189
5/20/78	1,316	840.08	17,800	4.72	10	10,711,026
6/17/78	1,370	570.66	19,885	2.87	11	7,650,064
8/15/78	1,489	815.00	25,610	3.18	13	12,206,888
Area III (Northwest Florida)						
8/8/77	508	9.24	944	0.98	1	196,938
8/8/77	568	11.95	1,318	0.91	1	160,722
8/7/77	608	24.70	1,950	1.27	1	404,982
7/2/78	652	39.53	2,497	1.58	1	688,354
8/14/77	727	105.96	3,180	3.33	2	1,640,497
7/14/77	780	139.64	3,424	4.08	—	2,102,579
6/27/78	816	301.26	4,450	6.64	—	5,049,856
8/7/78	826	167.31	4,903	3.41	2	2,912,649
6/19/77	862	186.02	4,680	3.98	4	2,509,948
7/4/78	906	210.33	5,630	3.74	6	3,005,716
6/27/78	929	96.05	6,492	1.48	—	1,891,588
7/13/77	980	205.49	8,170	2.52	—	3,346,332
7/20/77	1,018	268.22	12,700	2.11	—	4,960,702
6/19/77	1,087	602.45	11,350	5.31	7	5,744,230
8/24/77	1,108	476.06	9,768	4.87	—	5,836,910
9/5/78	1,142	538.60	12,031	4.48	8	8,070,585
8/14/78	1,220	575.39	14,437	3.99	7	7,489,089
Area IV (North Carolina)						
7/13/77	617	171.17	5,765	2.97	—	2,625,338
9/9/78	780	131.11	3,632	3.61	3	1,667,418
7/28/78	841	207.22	5,766	3.59	4	2,330,248
9/21/78	844	100.07	4,722	2.12	4	969,206
7/26/78	865	150.50	4,631	3.25	—	1,639,189
7/15/78	869	227.67	4,767	4.78	—	2,795,451
9/9/78	880	119.88	4,858	2.47	5	1,236,055
7/1/78	900	170.57	6,628	2.57	4	3,321,377
8/27/78	972	214.00	7,173	2.98	6	3,204,055
8/27/78	996	282.01	7,718	3.65	6	2,652,453
9/9/78	1,000	267.35	6,992	3.82	8	2,797,301
8/30/78	1,050	416.04	9,988	4.17	8	6,102,347

TABLE 4.—Regressions of fecundity (F) on total weight (TW), fork length (FL), and age (A) of king mackerel by areas.

Area	Predictor	Equation	r^2
I	TW	$F = 8.554 \times 10^{1}(TW)^{1.465}$	0.745
(TX)	FL	$F = 8.816 \times 10^{-7}(FL)^{4.206}$	0.781
	A	$F = 2.487 \times 10^{5}(A)^{1.390}$	0.373
II	TW	$F = 1.475 \times 10^{1}(TW)^{1.381}$	0.847
(LA-MS)	FL	$F = 9.973 \times 10^{-7}(FL)^{4.175}$	0.840
	A	$F = 4.207 \times 10^{5}(A)^{1.313}$	0.721
III	TW	$F = 1.327 \times 10^{1}(TW)^{1.408}$	0.877
(NWF)	FL	$F = 1.918 \times 10^{-7}(FL)^{4.455}$	0.884
	A	$F = 4.684 \times 10^{5} + 9.494 \times 10^{5}(A)$	0.870
IV	TW	$F = 1.419 \times 10^{6} + (6.658 \times 10^{2})TW$	0.760
(NC-SC)	FL	$F = -2.554 \times 10^{6} + (5.840 \times 10^{3})FL$	0.257
	A	$F = -2.778 \times 10^{5} + (5.579 \times 10^{5})A$	0.436
I-IV	TW	$F = 1.854 \times 10^{1}(TW)^{1.361}$	0.856
(All areas)	FL	$F = 4.391 \times 10^{-6}(FL)^{3.974}$	0.820
	A	$F = 3.399 \times 10^{5}(A)^{1.356}$	0.730

Williams and Godcharles[5] have postulated on the basis of mark-recapture data that two migratory groups occur: one in the South Atlantic and the other in the Gulf of Mexico. Both of their ranges overlap in south Florida.

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LITERATURE CITED

ALVES, M. I. M., AND G. S. TOME.
1967. Alguns aspectos do desenvolvimento maturativo das gonadas da cavala, *Scomberomorus cavalla* (Cuvier, 1829). Arq. Estac. Biol. Mar. Univ. Fed. Ceara 7(1):1-9.

BAGLIN, R. E., JR.
1982. Reproductive biology of western Atlantic bluefin tuna. Fish. Bull., U.S. 80:121-134.

BEAUMARIAGE, D. S.
1973. Age, growth, and reproduction of king mackerel, *Scomberomorus cavalla*, in Florida. Fla. Mar. Res. Publ., No. 1, 45 p.

BRUSHER, H. A., L. TRENT, AND M. L. WILLIAMS.
1978. Recreational fishing for king mackerel in Bay County, Florida during 1975. *In* C. B. Austin et al. (editors), Mackerel Workshop Report, p. 120-142. Univ. Miami Sea Grant, Spec. Rep., No. 14.

CLARK, F. N.
1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Dep. Fish Game, Fish Bull. 42, 49 p.

COLLETTE, B. B., AND J. L. RUSSO.
1979. An introduction to the Spanish mackerels, genus *Scomberomorus*. *In* E. L. Nakamura and H. R. Bullis, Jr. (editors), Proceedings of Colloquium on the Spanish and King Mackerel Resources of the Gulf of Mexico, p. 3-16. Gulf States Marine Fisheries Commission. No. 4.
1984. Morphology, systematics, and biology of the Spanish mackerels (*Scomberomorus*, Scombridae). Fish. Bull., U.S. 82:545-692.

DWINELL, S. E., AND C. R. FUTCH.
1973. Spanish and king mackerel larvae and juveniles in the northeastern Gulf of Mexico, June through October 1969. Fla. Dep. Nat. Resourc., Mar. Res. Lab., Leafl. Ser. 4 (pt. 1, no. 24), 14 p.

FINUCANE, J. H., AND L. A. COLLINS.
1977. Environmental assessment of an active oil field in the northwestern Gulf of Mexico, 1976-1977. Ichthyoplankton, NOAA Final Report to EPA, 150 p.
1984. Reproductive biology of cero, *Scomberomorus regalis*, from the coastal waters of south Florida. Northeast Gulf Sci. 7(1):101-107.

GESTEIRA, T. C. V., AND A. L. L. MESQUITA.
1976. Epoca de reproducao tamanho e idade na primeira desova da cavala e da serra, na costa do Estado do Ceara (Brasil). Arq. Cienc. Mar. 16(2):83-86.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

IVO, C. T. C.
1972. Epoca de desova e idade na primeira maturãcao sexual da cavala, *Scomberomorus cavalla* (Cuvier), no Estado do Ceara. Arq. Cienc. Mar. 12(1):27-29.
1974. Sobre a fecundidade da cavala, *Scomberomorus cavalla* (Cuvier), em águas costeiras do Estado do Ceará (Brasil). Arq. Cienc. Mar. 14(2):87-89.

JOHNSON, A. G., W. A. FABLE, JR., M. L. WILLIAMS, AND L. E. BARGER.
1983. Age, growth, and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States. Fish. Bull., U.S. 81:97-106.

MACGREGOR, R. M., III, J. J. DINDO, AND J. H. FINUCANE.
1981. Changes in serum androgens and estrogens during spawning in bluefish, *Pomatomus saltator*, and king mackerel, *Scomberomorus cavalla*. Can. J. Zool. 59:1749-1754.

MANOOCH, C. S., III.
1979. Recreational and commercial fisheries for king mackerel, *Scomberomorus cavalla*, in the South Atlantic Bight and Gulf of Mexico, U.S.A. *In* E. L. Nakamura and H. R. Bullis, Jr. (editors), Proceedings of Colloquium on the Spanish and King Mackerel Resources of the Gulf of Mexico, p. 33-41. Gulf States Marine Fisheries Commission No. 4.

MANOOCH, C. S., III, E. L. NAKAMURA, AND A. B. HALL.
1978. Annotated bibliography of four Atlantic scombrids: *Scomberomorus brasiliensis*, *S. cavalla*, *S. maculatus*, and *S. regalis*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 418, 166 p.

MCEACHRAN, J. D., J. H. FINUCANE, AND L. S. HALL.
1980. Distribution, seasonality and abundance of king and Spanish mackerel larvae in the northwestern Gulf of Mexico (Pisces: Scombridae). Northeast Gulf Sci. 4(1):1-16.

MENEZES, M. F.
1969. Alimentaçao da cavala, *Scomberomorus cavalla* (Cuvier), em águas costeiras do Estado do Ceará. Arq. Cienc. Mar. 9(1):15-20.

MOE, M. A., JR.
1963. A survey of offshore fishing in Florida. Fla. State Board Conserv. Mar. Lab., Prof. Pap. Ser. 4, 115 p.

MORSE, W. W.
1980. Spawning and fecundity of Atlantic mackerel, *Scomber scombrus*, in the Middle Atlantic Bight. Fish. Bull., U.S. 78:103-108.

OTSU, T., AND R. N. UCHIDA.
1959. Sexual maturity and spawning of albacore in the Pacific Ocean. Fish. Bull., U.S. 59:287-305.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics (with special references to biological sciences). McGraw-Hill Book Co., Inc., N.Y., 481 p.

U.S. DEPARTMENT OF COMMERCE, NATIONAL MARINE FISHERIES SERVICE.
1985a. Fisheries of the United States, 1984. Current Fishery Statistics 8360, 121 p.
1985b. Marine recreational fishery statistics survey, Atlantic and Gulf Coasts, 1983-1984. Current Fisheries Statistics 8326, 222 p.

[5]Williams, R. O., and M. F. Godcharles. Fisheries stock assessment, king mackerel tagging and stock assessment. Annual report for 1981-82. Florida Department of Natural Resources, Marine Research Laboratory, 100 Eighth Ave., S.E., St. Petersburg, FL 33701.

WOLLAM, M. B.
1970. Description and distribution of larvae and early juveniles of king mackerel, *Scomberomorus cavalla* (Cuvier), and Spanish mackerel, *Scomberomorus maculatus* (Mitchill), (Pisces: Scombridae) in the western north Atlantic. Fla. Dep. Nat. Resourc. Mar. Res. Lab. Tech. Ser. 61, 35 p.

YUEN, H. S. H.
1955. Maturity and fecundity of bigeye tuna in the Pacific. Spec. Sci. Rep. Fish. 150, 30 p.

NEW OCCURRENCE OF EPIZOOTIC SARCOMA IN CHESAPEAKE BAY SOFT SHELL CLAMS, *MYA ARENARIA*

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ABSTRACT

Maryland soft shell clams, *Mya arenaria*, from Chesapeake Bay were sampled from 1969 through January 1983. Four cases of sarcomatous neoplasia were diagnosed histologically [1979 (1), 1982 (2), January 1983 (1)] in 3,584 animals. Hemocytologic sampling between December 1983 and May 1984 revealed peak prevalences of 42-65% in clams from five sites. Sarcomas in laboratory-held clams progressed from early to advanced stages and death. This is the first time epizootic neoplastic disease has been observed in a wild molluscan population which was previously documented to be sarcoma-free. An infectious etiology is implied and data indicate the potential for mass mortality of bay clams.

Neoplastic diseases in soft shell clams, *Mya arenaria*, have been reported from New England populations in both polluted and nonpolluted areas (Barry and Yevich 1975; Farley 1976a; Yevich and Barszcz 1977; Brown et al. 1977, 1979; Brown 1980; Cooper et al. 1982a; Reinisch et al. 1984). Generally, the types of neoplasia noted have been considered as having hemocyte (blood cell) (Yevich and Barszcz 1977; Brown et al. 1977, 1979; Brown 1980; Cooper et al. 1982a; Reinisch et al. 1984) and gonadal (Barry and Yevich 1975; Yevich and Barszcz 1977; Brown et al. 1977, 1979; Brown 1980) origins or have been designated as sarcomatous (Farley 1976a). A single neoplastic clam was reported from Chesapeake Bay with an apparent teratoma composed of nerve and muscle tissue and digestive epithelium (Harshbarger et al. 1977). Chesapeake Bay soft clams collected and examined by several authors between 1971 and 1978 were free of the neoplastic disease (Barry and Yevich 1975; Brown 1980) with the exception of 1 case found in a collection of 3,000 clams used as experimental controls (Brown 1980). Evidence for a viral etiology for hematopoietic neoplasia in clams was reported in a Rhode Island study (Oprandy et al. 1981). Improved techniques such as examination of hemolymph using a combination of histologic and cytologic procedures (Cooper et al. 1982b) and the development of a monoclonal antibody test specific for neoplastic clam cells (Reinisch et al. 1983) have facilitated the identification and diagnosis of the disease. High prevalences of sarcomas have been found repeatedly in populations of Chesapeake Bay clams.

This paper documents the first occurrence of epizootic sarcoma in soft shell clams in Chesapeake Bay, and the first time neoplastic disease has appeared in a wild molluscan population that was previously shown to be free of the disease. Epizootic prevalences of this condition may have a potentially devastating impact on the clam industry of the region.

MATERIALS AND METHODS

Sixty samples of 25 or more soft shell clams (totaling over 3,500 clams) have been collected periodically by the Maryland Department of Natural Resources (DNR) or purchased from seafood outlets from 51 sites in Chesapeake Bay since 1969. Each animal was necropsied and tissues were fixed, processed, and diagnosed histologically via standard methods (Howard and Smith 1983) for diseases and parasites. Recent samples (Table 1) were examined by cytologic methods to determine the percent prevalence and number of abnormal cells. Late spring samples (YCLP, YSWP, YAGH, and YPIS, Table 1) were diagnosed by both histology and histocytology (technique described below).

Hemolymph was drawn via hypodermic syringe into sterile, ambient (15‰), artificial seawater to produce a 1:9 dilution of cells to seawater. One milliliter of this sample was placed on a 25 mm, chambered, poly-L-lysine coated microscope slide and cells were allowed to settle for 1 h (the poly-L-lysine coating improves the adhesiveness of neoplastic cells which in vitro are rounded and do not usually stick to glass [Cooper 1982a]). Fluid and chambers were

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TABLE 1.—Prevalence of sarcoma in recent and historic samples diagnosed from Feul
from archived State of Maryland samples. Clams were collected from

Location	Clam bed site	Date	Sample code	No. per sample	Adva sarco (stage (%
Commercial sample	Site unknown	6 Dec. 1983	OXC	18	1
Commercial sample	Site unknown	8 Dec. 1983	EBC	16	1(
Commercial sample	Site unknown	1 Feb. 1984	KNC	74	1
Chester River	Long Point	19 Apr. 1984	YCLP	50	
Chester River	Swan Point	19 Apr. 1984	YSWP	50	2
West River	Three Sisters	4 May 1984	YAGH	50	5
Eastern Bay	Poplar Island	4 May 1984	YPIS	50	5
Total sample data				308	
Chester River	Swan Point	28 June 1984	YSWP 2	50	
Eastern Bay	Poplar Island	July/Aug. 1984	YPIS	50	
Chester River	Swan Point	July/Aug. 1984	YSWP 3	40	
Eastern Bay	Poplar Island	26 Oct. 1984	YPIS	50	3
Chester River	Swan Point	26 Oct. 1984	YSWP 5	50	4
Chester River	Swan Point	7 Jan. 1985	YSWP 1	68	4
Chester River	Swan Point	29 Mar. 1985	YSWP 2	52	6
Chester River	Swan Point	17 May 1985	YSWP 3	52	1(
					Historic archived sa
Choptank River, Eastern Bay & Chester River		Dec.-May 1969-78		362	
Little Choptank River & West River		1979-Jan. 1983		250	

n Feulgen-stained cytologic and histologic preparations in recent samples and
ed from 1969 through October 1984 from comparable areas.

Advanced sarcomas (stages 4, 5) (%)	Advanced sarcomas in sample (stages 4, 5) (%)	Prevalence diagnosed by histocytology (%)	Prevalence diagnosed by histology (%)	Combined prevalence
13	6	44	—	—
100	6	6	—	—
18	4	23	—	—
0	0	0	0	0
24	10	46	32	46
56	28	50	52	57
52	24	42	27	42
			31 (%/200) = 29.5	
0	0	0	—	—
0	0	0	—	—
0	0	3	—	—
35	12	32	—	—
47	14	25	—	—
40	32	59	—	—
60	39	65	—	—
100	15	15	—	—
ved samples				
			0	
			1.6	

removed, while slides were wet-fixed in an aldehyde fixative (1% glutaraldehyde/4% formaldehyde) (McDowell and Trump 1976) in half ambient seawater and stained with Feulgen picromethyl blue (Farley 1969), dehydrated, and mounted with a coverslip using a synthetic mounting medium. We are designating the term "histocytology" to describe this technique. The significance of this method is that the monolayer preparations, which result from treating living cells with histologic procedures, are permanent. Cytologic artifacts are minimal and cases can be accurately staged using cell counting procedures. Since histocytologic preparations contain between 100,000 and 500,000 cells in a monolayer, very early stages of the proliferative process can be diagnosed. Staging is arbitrarily determined by estimating the number and determining the ratio of both normal and neoplastic cells (Table 2). A similar diagnostic and staging method using cytologic techniques was reported by Cooper et al. (1982b); however, our method appears to have better accuracy and increased sensitivity to light cases. Diagnosis of histologic sections is reliable for stages 3-5 (Fig. 1A). As an example, comparison of late spring samples shows that histocytology is the more sensitive method while histology alone clearly demonstrates a massive increase in prevalence from zero in 1969-78 to 29.5% in 1984 (Table 1).

Monoclonal antibody was developed against neoplastic clam cells from Massachusetts clams by techniques described elsewhere (Reinisch et al. 1983). Periodic histocytologic diagnosis and mortality observations were made on clams held in 55 L aquaria with 15‰, 10°C artificial seawater, circulated through floss and charcoal filtering systems.

RESULTS

Sarcomas in clams were diagnosed histologically in 1/25 in November 1979 from Eastern Bay; 1/25 in May 1981 from West River; 1/50 in November 1981 from Little Choptank River; and 1/75 in January 1983 from Chester River. In December 1983, histocytologic diagnoses of clams obtained from a local seafood restaurant showed 8/18 with sarcomas.

An intensive survey and study of local populations was initiated in December 1983 to evaluate the extent of this apparently new epizootic in Chesapeake Bay soft shell clams. Table 1 presents epizootiology of field collections while Table 2 shows comparable information on laboratory-held clams. Field prevalences were found to be high in most samples from December 1983 through April 1985. At the same time, disease intensities which were light in Decem-

TABLE 2.—Sarcoma progression in individual, laboratory-held soft shell clams: Dec. 1983-June 1984. Whole numbers = percent ratios of neoplastic cells to hemocytes and numbers in parentheses = stages of disease. Stages: Early (1) = 0.01-0.09% and (2) = 0.1-0.9%; Intermediate (3) = 1-49%; Advanced (4) = 50-89% and (5) = 90-100%. (Diagnosed from Feulgen-stained cytologic preparations.)

Date	Specimen data										Sample data			
											Neoplastic clams		Normal clams	
	OXC 1	OXC 2	OXC 4	OXC 8	OXC 10	OXC 11	OXC 13	OXC 1	OXC 18	EBC 6	Advanced cases (%) (*N* = 10)	Cumulative mortality (%) (*N* = 10)	Cumulative mortality (%) (*N* = 20)
6 Dec. 1983	70(4)	0.5(2)	0.01(1)	(0)	0.02(1)	12(3)	0.5 (2)	0.1(2)	(0)	—	14	0	0
12 Dec. 1983	78(4)	6 (3)	—	0.03(1)	—	10(3)	0.96(2)	—	—	5(3)	11	0	0
19 Dec. 1983	Died	11 (3)	29 (3)	0.9 (2)	0.1 (2)	Died	1 (3)	0.8(2)	(0)	62(4)	14	20	5
3 Jan. 1984		33 (3)	16 (3)	2 (3)	8 (3)		33 (3)	0.9(2)	(0)	50(4)	14	20	15
16 Jan. 1984		40 (3)	50 (4)	8 (3)	8 (3)		25 (3)	0.1(2)	0.1(2)	67(4)	25	20	15
30 Jan. 1984		80 (4)	50 (4)	10 (3)	2 (3)		17 (3)	0.8(2)	0.1(2)	57(4)	38	20	20
22 Feb. 1984		90 (5)	80 (4)	53 (4)	2 (3)		70 (4)	5 (3)	0.1(2)	95(5)	63	20	25
3 Apr. 1984		95 (5)	90 (5)	85 (4)	40 (3)		92 (5)	8 (3)	10 (3)	95(5)	63	20	25
13 Apr. 1984		Died	98 (5)	99 (5)	Died		98 (5)	12 (3)	62 (4)	99(5)	83	40	40
May 1984			Died				Died			Died	—	70	50
June 1984				Died				Died	Died		—	100	55

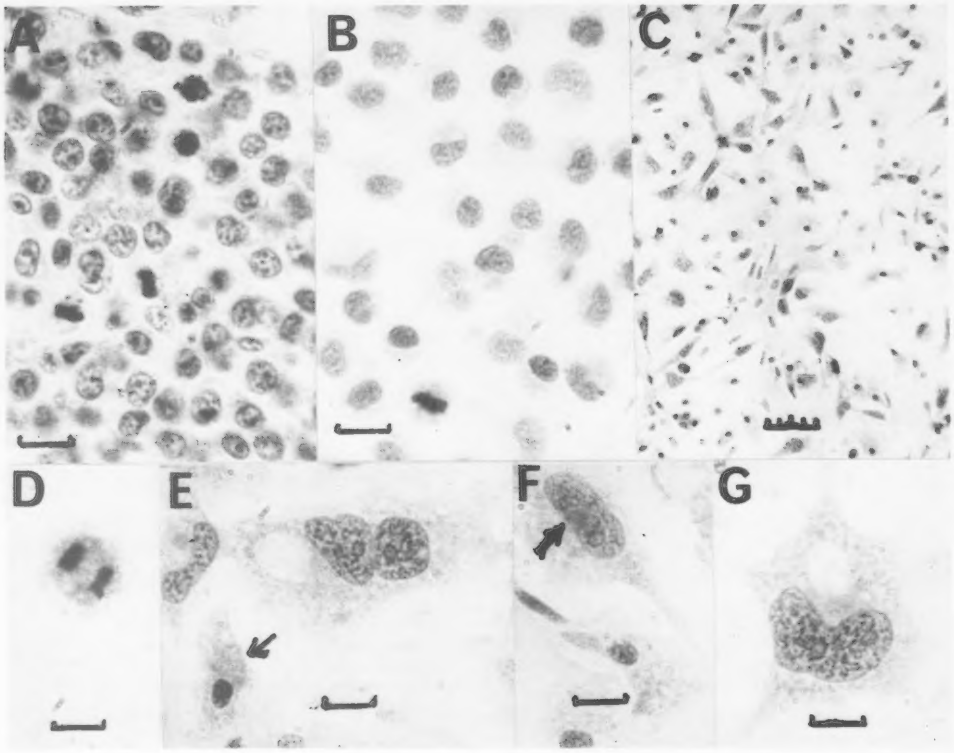

FIGURE 1.—Cytology of clam sarcoma, 1 unit = 10 μm. (A) Histologic section: Note large, hyperchromatic nuclei, abundant mitotic figures and metaphase with laggard chromosomes. (B-G) Histocytologic preparations: (B) Stage 5 (all cells neoplastic); rounded cells show mitosis and large, reniform, hyperchromatic nuclei. (C) Stage 3 sarcoma; about 10% of the cells are neoplastic. Compare sizes of normal (small) and neoplastic (large) nuclei. (D) Mitotic figure in anaphase. (E) Binucleate neoplastic cell with prominent, multiple nucleoli (normal hemocyte, arrow). (F) Neoplastic cell with intranuclear inclusion (arrow). (G) Very large neoplastic cell with nucleus and prominent Golgi zone.

ber progressed to advanced and terminal stages by April in laboratory-held animals. This situation was reflected in the field by an increase in the prevalence of advanced cases as the season progressed. The higher histologic prevalence in the YAGH sample was due to four positive cases from sections of dead animals which were not diagnosable by histocytology. This information provides additional evidence of mortality in feral populations. Cooper et al. (1982a) demonstrated in laboratory experiments the lethal nature of this disease in animals with advanced cases and noted similar implications in field monitored populations. A chronic phase with remission was reported by Cooper, but these features were not evident in the Chesapeake Bay epizootic. It is conceivable that some resistance has developed in the long-term occurrence of this disease over generations of clams in New England. Selection has not, as yet, had a chance to develop resistant animals in Chesapeake Bay. The mortality which began in laboratory-held animals in April was 100% by the end of June (Table 2). Field prevalences also dropped to zero in June. Sarcomas reappeared in the population in October.

Neoplastic clam cells from OXC 1 and EBC 6 (Table 2) were incubated with the murine monoclonal antibody IE7 which is specifically reactive with Massachusetts *Mya* neoplastic cells (Reinisch et al. 1983). Upon fluorescence activated cell sorter analyses, neoplastic cells from OXC 1 (Fig. 2) and EBC 6 were positive when stained with IE7.

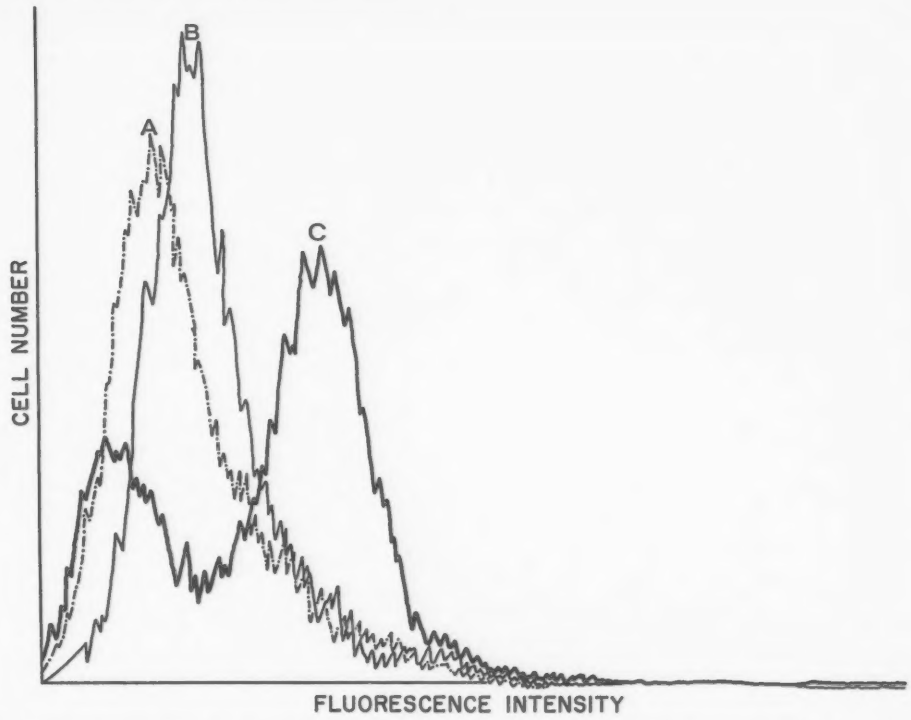

FIGURE 2.—OXC 1 cells were fixed in 0.1% neutral formaldehyde. Following three washes in sterile seawater, the cells were then incubated with: (A) a 1:50 dilution of fluoresceinated (FITC) goat and antimouse IgG antibody (-·-·-·), (B) a 1:100 dilution of heat-inactivated normal mouse serum, and subsequently with a 1:50 dilution of FITC-goat antimouse IgG antibody (——), or (C) monoclonal antibody IE7, and subsequently with a 1:50 dilution of FITC-goat antimouse IgG antibody (——). All the antisera were diluted in sterile seawater immediately prior to use. The samples were then evaluated by a Becton-Dickinson Fluorescence Activated Cell Sorter IV (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA).

DISCUSSION

Epizootiology

Laboratory and field observations complement each other and confirm the suspicion that affected animals die from the disease. Individual diseased clams monitored in aquaria from early December 1983 to May 1984 had progressed from early stages 1 and 2 to advanced stages 4 and 5 with 100% mortality. The high prevalences and advancing stages seen in natural populations may signal significant, impending mortalities. Samples collected from Swan Point (YSWP) in July and August 1984 (Table 1) showed 1/15 and 0/25 sarcomas, respectively. Samples from Poplar Island in July and August were 0/25 and 0/25. High sarcoma prevalences reappeared in the fall in smaller clams at Swan Point (25%) and Poplar Island (32%) in October. The decrease in prevalence to zero corresponds with observations of laboratory-held animals, suggesting that the disease was also 100% fatal in field populations. The experiments of Brown (1980) and others (Oprandy et al. 1981) indicate an infectious etiology for the disease. The nature of the new situation in Chesapeake Bay suggests that an infectious agent may have been established in clams by introduction from New England, since previous information indicated that the disease was confined to sites north of New Jersey (Barry and Yevich 1975; Yevich and Barszcz 1977; Brown et al. 1977, 1979; Brown 1980; Koepp 1984). Introductions of clams from New England to

Maryland have been documented in the past (post-tropical storm Agnes in 1972) (S. V. Otto unpubl. data). Antigenic similarity between neoplastic clams in New England and Maryland suggests that target cells in the disease are the same in both areas. Additionally, the sudden appearance of isolated occurrences of the disease in widespread areas of the Bay and the apparent tenfold increase in frequencies since its appearance in 1978 in populations occurring over most of the geographic range of soft clams in the Bay suggest an infectious etiology rather than point source chemical oncogen activity or pollution (Barry and Yevich 1975; Yevich and Barszcz 1977; Cooper et al. 1982a; Reinisch et al. 1984) as has been implied in some New England studies.

Classification

Histologically, the clam sarcomas (Fig. 1A) consist of diffusely disseminated round cells with a large, 6-10 μm, hyperchromatic, often lobed nucleus containing one or more prominent nucleoli. Cytoplasm is sparse, mitosis is common, and nuclei are more than twice as large as normal hemocyte nuclei. Histocytologic preparations (Fig. 1B-G) reveal sarcoma cells with identical characteristics and which can be definitively recognized on the basis of their morphology.

Other authors (Yevich and Barszcz 1977; Brown et al. 1977; Reinisch et al. 1983) have called this disease a "hematopoietic neoplasm" because of the general similarity of neoplastic cells and hemocytes, and because of its occurrence in vascular spaces. While this is the most probable origin for these cells, previous studies in other species have shown that these criteria can be misleading. The neoplasm in *Macoma balthica* (Christensen et al. 1974), which was characterized by anaplastic cells inhabiting the vascular spaces, was shown ultrastructurally to be of epithelial origin and, therefore, diagnosable as a carcinoma (Farley 1976b). Since no specific identifying organelles have been seen in the soft clam neoplasm (Brown et al. 1977) and since some monoclonal antibodies developed against neoplastic cells do not cross react with normal hemocytes, we prefer the more conservative term "sarcoma" which identifies the disease by behavior and cytology but does not imply a particular cell origin. These data indicate disease irreversibility and satisfy most of the other criteria for sarcoma or carcinoma, namely: 1) loss of cell specialization (anaplasia); 2) cell proliferation; 3) invasiveness (diffuse infiltration of connective tissue and muscle); 4) clonal alteration of genetic material (probable polyploidy evidenced by enlarged, hyperchromatic nuclei); and 5) clinical features such as progression and malignancy.

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LITERATURE CITED

BARRY, M. M., AND P. P. YEVICH.
1975. The ecological, chemical and histopathological evaluation of an oil spill site: Part III. Histopathological studies. Mar. Pollut. Bull. 6:171-173.

BROWN, R. S.
1980. The value of the multidisciplinary approach to research on marine pollution effects as evidenced in a three-year study to determine the etiology and pathogenesis of neoplasia in the soft-shell clam, *Mya arenaria*. Rapp. P.-v. Réun. Cons. int. Explor. Mer 179:125-128.

BROWN, R. S., R. E. WOLKE, S. B. SAILA, AND C. W. BROWN.
1977. Prevalence of neoplasia in 10 New England populations of the soft-shell clam (*Mya arenaria*). Ann. N.Y. Acad. Sci. 298:522-534.

BROWN, R. S., R. E. WOLKE, C. W. BROWN, AND S. B. SAILA.
1979. Hydrocarbon pollution and the prevalence of neoplasia in New England soft-shell clams (*Mya arenaria*). *In* Animals as monitors of environmental pollutants, p. 41-51. National Academy of Sciences, Washington, D.C.

CHRISTENSEN, D. J., C. A. FARLEY, AND F. G. KERN.
1974. Epizootic neoplasms in the clam *Macoma balthica* (L.) from Chesapeake Bay. J. Natl. Cancer Inst. 52:1739-1749.

COOPER, K. R., R. S. BROWN, AND P. W. CHANG.
1982a. Accuracy of blood cytological screening techniques for the diagnosis of a possible hematopoietic neoplasm in the bivalve mollusc, *Mya arenaria*. J. Invertebr. Pathol. 39: 281-289.
1982b. The course and mortality of a hematopoietic neoplasm in the soft-shell clam, *Mya arenaria*. J. Invertebr. Pathol. 39:149-157.

FARLEY, C. A.
1969. Probable neoplastic disease of the hematopoietic system in oysters, *Crassostrea virginica* and *Crassostrea gigas*. Natl. Cancer Inst. Monogr. 31:541-555.
1976a. Proliferative disorders in bivalve mollusks. Mar. Fish. Rev. 38(10):30-33.
1976b. Ultrastructural observations on epizootic neoplasia and lytic virus infection in bivalve mollusks. Prog. Exp. Tumor Res. 20:283-294.

HARSHBARGER, J. C., S. V. OTTO, AND S. C. CHANG.
1977. Proliferative disorders in *Crassostrea virginica* and *Mya arenaria* from the Chesapeake Bay and intranuclear virus-like inclusions in *Mya arenaria* with germinomas from a Maine oil spill site. Haliotis 8:243-248.

HOWARD, D. W., AND C. S. SMITH.
1983. Histological techniques for marine bivalve mollusks. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NEC 25, 97 p.

KOEPP, S. J.
1984. Detection of a DNA virus within an upper New York Bay soft-shell clam population. Coastal Ocean Pollut. Assess. News 3:26-28.

MCDOWELL, E. M., AND B. F. TRUMP.
1976. Histologic fixatives suitable for diagnostic light and electron microscopy. Arch. Pathol. Lab. Med. 100:405-414.

OPRANDY, J. J., P. W. CHANG, A. D. PRONOVOST, K. R. COOPER, R. S. BROWN, AND V. J. YATES.
1981. Isolation of a viral agent causing hematopoietic neoplasia in the soft-shell clam, *Mya arenaria*. J. Invertebr. Pathol. 38:45-51.

REINISCH, C. L., A. M. CHARLES, AND J. TROUTNER.
1983. Unique antigens on neoplastic cells of the soft shell clam *Mya arenaria*. Dev. Comp. Immunol. 7:33-39.

REINISCH, C. L., A. M. CHARLES, AND A. M. STONE.
1984. Epizootic neoplasia in soft shell clams collected from New Bedford Harbor. Hazardous Waste 1:73-81.

YEVICH, P. P., AND C. A. BARSZCZ.
1977. Neoplasia in soft-shell clams (*Mya arenaria*) collected from oil-impacted sites. Ann. N.Y. Acad. Sci. 298:409-426.

SIZE-SPECIFIC VULNERABILITY OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY FISHES

ARILD FOLKVORD[1] AND JOHN R. HUNTER[2]

ABSTRACT

Vulnerability of larval northern anchovy (6-33 mm SL) to predation by adult northern anchovy and juvenile chub mackerel, *Scomber japonicus*, was estimated by measuring the response and escape probabilities of larvae. The proportion of larvae responding to the attacks of either predator increased with larval length and differed little between predator species. About 20% of 6 mm larvae responded to attacks of predators while 85-100% of 33 mm larvae responded. The proportion of larvae escaping attacks also increased with larval length, but more larvae of all sizes escaped the attacks of adult northern anchovy than those of juvenile chub mackerel. The rate of consumption of northern anchovy larvae by adult northern anchovy was highest when the larvae were 8.5-15 mm long, indicating that greater avoidance success of larvae in this size range relative to smaller ones may not completely compensate for their greater visibility to predators.

The events that cause variation in year-class strength in marine fish stocks occur during the first year of life, but no single life stage or period has been identified as being uniquely influential in the establishment of year classes. Mortality rates are size specific over this period with rates being the highest during the egg and yolk-sac stages and declining thereafter (Hunter 1984; Smith 1985). Variation in the relatively low mortality rates of older larval and juvenile stages may be more influential in year-class formation than the variation of the high mortality rates of eggs and first feeding larvae (Smith 1985). Thus all early life stages from egg through juvenile must be considered and knowledge of the size- or age-specific vulnerability of larvae to predation and starvation is central in any attempt at modeling the recruitment process.

Starvation is probably a direct source of larval mortality for only a few weeks after the onset of feeding, and most losses in the first year of life may be attributed to predation. Predation is believed to be the major cause of mortality during the egg and yolk-sac stages (Hunter 1984), and incidence of starving jack mackerel, *Trachurus symmetricus*, and northern anchovy, *Engraulis mordax*, in the sea indicate that significant starvation mortality is restricted to the first 1-2 wk of feeding or about 10-20% of the larval period (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986). The vulnerability of larvae to predation has been studied over limited size ranges; laboratory data indicate that yolk-sac larvae seem to be vulnerable to small invertebrate predators (copepods, amphipods, and euphausiids [Hunter 1984]). In addition, some egg and larval predators have been identified in field studies and in several cases loss rates due to predation have been estimated (Möller 1984; Frank and Leggett 1984; Van der Veer 1985; Purcell 1985; older literature summarized by Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of northern anchovy larvae to predation by pelagic fishes. The size-specific vulnerability of larval Cape anchovy, *E. capensis*, to cannibalism has been investigated by Brownell (1985) and vulnerability of larval *E. mordax* to predation by the aquarium fish *Amphiprion percula* was studied by Webb (1981). The results of the current study will be compared to these papers in the discussion.

Our approach was to observe the avoidance behavior of northern anchovy larvae in response to predatory attacks by adult northern anchovy and juvenile chub mackerel, *Scomber japonicus*. Adult northern anchovy were selected as a predator because it is the most abundant fish stock in the California Current region and because it has a planktivorous diet which includes fish eggs and larvae (Baxter 1967; Hunter and Kimbrell 1980). Chub

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mackerel is also a major fish stock in the region and is both planktivorous and piscivorous, with juvenile and adult northern anchovy being a dominant item in the diet of larger individuals (Schaefer 1980; Hunter and Lynn, unpubl. data, Southwest Fisheries Center, La Jolla, CA).

MATERIALS AND METHODS

Experimental Fishes

The northern anchovy larvae used in the experiments were reared from the egg; 2,000-7,000 eggs, from a laboratory brood stock (Leong 1971), were stocked in 400 L black circular fiberglass tanks containing about 150 L of filtered seawater. The culture methods of Hunter (1976) were used to rear the larvae, with extra additions of wild zooplankton when the larvae were 10-25 mm SL. Temperature in the rearing tanks was maintained at about 18°C (range, 17.2°-19.2°C).

Three groups of 5 adult northern anchovy (range of mean standard length [SL] = 8.3-8.9 cm) and a single group of 3 juvenile chub mackerel (mean SL = 19.1 cm) were used as predators. They were fed mainly adult brine shrimp and occasionally northern anchovy larvae. The predators were not fed for 10 h before an experiment.

Apparatus

Predators were kept in two rectangular fiberglass tanks (0.75 m × 2.15 m × 0.83 m = 1.35 m^3) with a clear glass window on one side for observation. Two 100 W tungsten household lamps produced 2,000-3,000 mc at the surface of each tank and a black plastic tent enclosed the window, providing a darkened compartment for an observer. Larvae were released into the tank by gently submerging a beaker at the water surface. Horizontal and vertical metric scales on the tank window aided estimation of predator attack distances. The tanks were continuously supplied with ambient seawater ranging from 20.5° to 23.8°C, except during an experiment when the water was static.

Experimental Procedure

It was necessary to measure the feeding performance of predators fed a standard prey because 1) adult northern anchovy are easily frightened and fright behavior reduces feeding motivation; 2) feeding could be affected by satiation during an experiment; and 3) feeding could be affected by the fish learning and responding to cues associated with the introduction of food. We used live adult brine shrimp (*Artemia* sp., 6.4 mm mean total length, standard deviation [SD] 1.2 mm, n = 25) as a standard prey. Variation in feeding performance of the predators could be more easily detected when *Artemia* were used because unlike the larvae the *Artemia* did not vary in size among experiments nor did they avoid attack by the predators.

Northern anchovy larvae and the adult *Artemia* were added to the tank in groups of three. An addition of three of either prey constituted a trial. A trial ended after 5 min or when all prey were taken. During a trial we used a computer compatible event recorder to record observations of the interactions between predator and prey. All the experiments using northern anchovy as predators started with 5 consecutive trials in which 3 *Artemia* were offered per trial. This was done to insure that northern anchovy predator groups had a similar level of feeding motivation. Preliminary experiments indicated that it normally took a few feeding trials before adult northern anchovy fed consistently. After the 5 initial trials, predators were offered fish larvae and adult *Artemia* alternately for 4-10 trials. Adult *Artemia* were always used in the last trial to determine if satiation had occurred. A less rigorous schedule was used for the chub mackerel predators because their feeding behavior was less variable than that of the northern anchovy. After 3 initial *Artemia* trials, the chub mackerel were given 5 larval trials followed by an *Artemia* trial. In most cases, a second set of 5 larval trials were also given and these were followed by a final *Artemia* trial to check if satiation had occurred.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. This number exceeded the number of larvae tested in many cases because, if a larva escaped the first encounter with a predator, the subsequent encounter was also recorded as an event. The total number of observations (predatory events) per larval size class (mean SL), when northern anchovy were the predators, was 5.9 mm, 24; 8.5 mm, 55; 11 mm, 48; 15 mm, 53; 21 mm, 82; and 33 mm, 62. Those for the chub mackerel experiments were 6.7 mm, 19; 10 mm, 75; 16 mm, 54; 21 mm, 27; 31 mm, 47; and 50 mm, 39.

Classification of Behavior

Prey behavior was recorded only when the predator attacked a prey. An attack was defined as

a movement directed toward the prey with the mouth open. During an attack the northern anchovy predator usually increased its swimming speed, but the chub mackerel increased speed only when attacking larvae larger than 10 mm SL.

Four measures of predator-prey interactions were calculated: mean and maximum attack distance; frequency of avoidance responses; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). The attack distance was the distance in decimeters (dm) from the prey to the point where the predator started the attack. An avoidance response was a change in speed or direction of a larva occurring before the predator had completed the attack by closing its mouth.

An escape was defined as a larval response in which the predator failed to capture the larva during a single attack. Repeated attacks were scored as separate events. By definition, adult *Artemia* could not be credited with an escape since they did not respond to an attack. Cases where attacked *Artemia* were not captured were considered predator errors. Predator error could only be assessed for *Artemia*. All interactions between predators and larvae in which the larvae were not captured were recorded as an escape.

Predator Performance

The feeding success and variation in feeding rates of predator groups fed live adult *Artemia* were analyzed to estimate predator error and to determine if differences existed in feeding performance among predator groups, or among or within experiments. An experiment was 2-5 larval trials conducted on a single size class of larvae on one day using a single predator group.

Predator errors were obvious when *Artemia* were the prey because *Artemia* did not avoid the attack. In such cases the trajectory of the attack was inaccurate and the predator simply missed the prey. Such errors occurred in 3.4% of the attacks on *Artemia*; this estimate is similar to error rates estimated for other predators (Curio 1976). We could not measure the predator error when larvae were the prey because we attributed any failure to capture a larva to larval avoidance success. Presumably our estimates of larval escape probabilities include an unknown number of cases where failure to capture a larva was the direct result of inaccuracies in the predator's attack rather than being the result of larval avoidance.

Considering all northern anchovy predator groups, predator error in capturing *Artemia* was higher in the first 5 trials than in the subsequent trials of the experiments where *Artemia* trials were alternated with larval trials (Fig. 1A). Predator error averaged 3.4% for all *Artemia* trials, whereas it was 2.1% during the period of alternating larval and *Artemia* trials. Similarly, adult northern anchovy took more time to capture all the *Artemia* in the first trial than in subsequent ones (Fig. 1B). No decline in feeding performance on *Artemia* existed at the end of the experiments, indicating that satiation did not constitute a bias in the experiments. The initial decline in the time required for northern anchovy predators to capture *Artemia* may have been caused by an increase in feeding motivation, learning, or a decrease in fright behavior. As the decline occurred during only the initial 5 *Artemia* trials, the larval data were probably unaffected.

Minor differences in feeding performance also existed among predator groups. In two experiments northern anchovy predatory groups fed markedly less on both *Artemia* and larvae (30% fewer prey taken in 5 min; t-test, $P < 0.05$). The effect of omitting these two experiments is indicated in the results. Overall, comparisons of feeding performance among groups, within trials, and among experiments indicated that variation in predator performance as measured by predation rates on *Artemia* was not significantly biased (additional details are given by Folkvord 1985) (see also Figure 1).

RESULTS

Probability of a Response to Predators

The most striking feature of the vulnerability of the youngest larval stages of northern anchovy to predators was the low frequency of escape attempts. Only 16% of the 6 mm larvae responded to the attacks of northern anchovy predators (Fig. 2B) and only 26% of 6.7 mm larvae responded to chub mackerel predators (Fig. 3B). The probability of smaller larvae (SL <20 mm) responding to either chub mackerel or northern anchovy predators was about the same (Fig. 4), although size, feeding behavior, and body form of these two fishes were distinctly different. The tendency to respond to attacking predators steadily increased with larval size until by the time northern anchovy larvae were 30 mm all attempted to avoid attacking northern anchovy and over 80% responded to chub mackerel attacks.

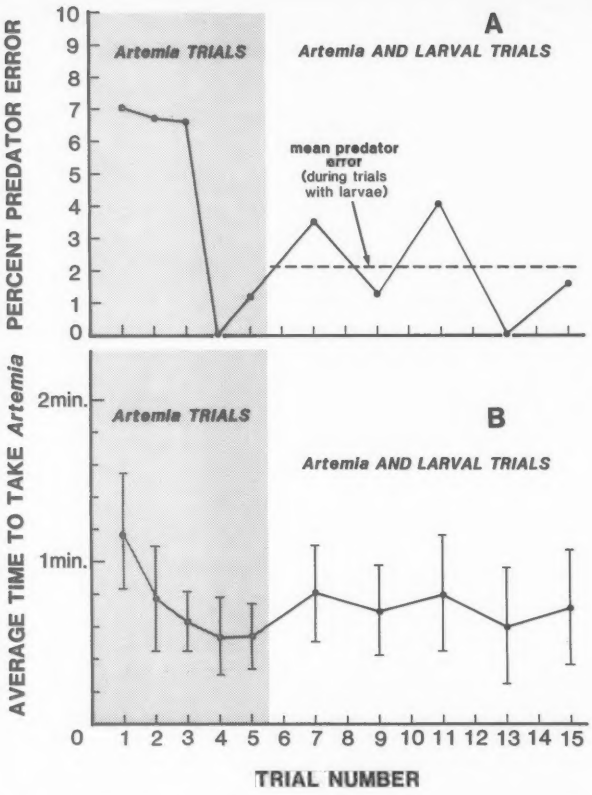

FIGURE 1.—Variation in feeding performance of northern anchovy predators fed live *Artemia* as a function of trial number (equivalent to elapsed time of experiment); shaded area indicates trials in which northern anchovy were fed only *Artemia*; unshaded areas, *Artemia* trials alternated with larval trials. A, percent predator error in capturing adult *Artemia* (percentage of attacks in which a northern anchovy missed the prey); dashed line indicates mean. B, mean time required for predator group to capture 3 adult *Artemia*; bars are 2 × SE of the mean. (N = 21.)

Success of Avoidance Movements

Larval vulnerability depended not only on the responsiveness but also on the success of avoidance movements. The proportion of larvae escaping northern anchovy predators increased from 8% for 6 mm larvae to 92% for 33 mm larvae with an estimated 50% of the 17 mm larvae escaping. The percentage of larvae escaping the attacks of chub mackerel was lower than for adult northern anchovy, but the curves given in Figures 2 and 3 had a similar form. Weibull curves were fit to the data to provide trend lines (equations and parameters given in Figure legends). The fraction of larvae that escaped increased from 6% of 6.7 mm larvae to an estimated 50% of the 30 mm larvae. Of the 50 mm juvenile northern anchovy used as prey only 64% escaped the attacks of the chub mackerel.

The ability to successfully avoid predator attacks was strongly affected by species-specific differences in predator behavior since the fraction of larvae escaping the attacks of northern anchovy increased much more rapidly with larval length than did the fraction escaping the attacks of chub mackerel. In contrast, the fraction of smaller larvae (SL <20 mm) responding to the attacks of these two predators was similar (Fig. 4). This indicates that probability of a larva responding to an attack is less affected

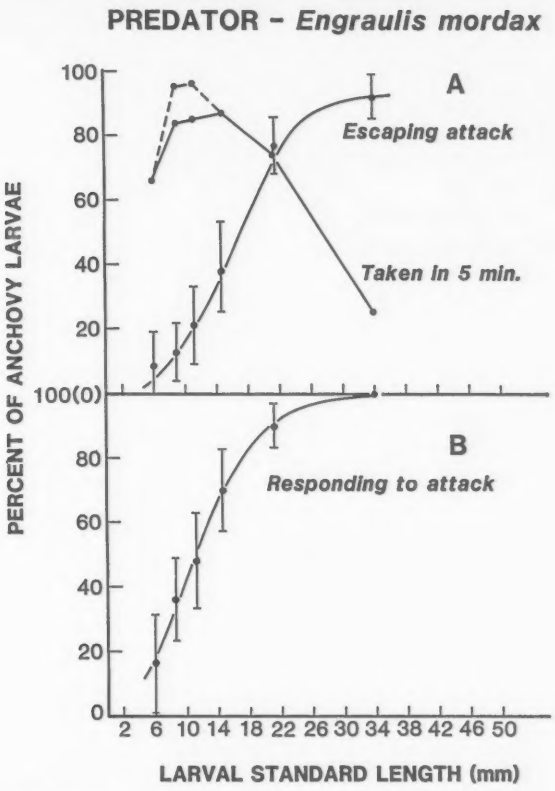

FIGURE 2.—Vulnerability of northern anchovy larvae to adult northern anchovy predators as a function of larval length. A, Percentage of northern anchovy larvae escaping attack; bars are 2 × SE; line is Weibull curve fit to six points using Marquardt's least squares method (Pielou 1981); equation is $N = K(1 - \exp(1 - (L/b) - \lambda))$ where $K = 0.93$, $b = 17.85$, $\lambda = 2.85$, N is the percentage of larvae and L = larval length; and predation rate of the northern anchovy predators (percentage eaten in 5 min) where dashed line is data when experiments with biased predator feeding motivation are omitted. B, Percentage of northern anchovy larvae that responded to the attack of an adult northern anchovy; bars are 2 × SE; and Weibull parameters for curve are $K = 1.00$, $b = 13.58$, and $\lambda = 1.94$.

by differences in predator behavior than is its success in avoiding the attack.

The success of avoidance movements can be separated from larval responsiveness by calculating the avoidance success of responding larvae (numbers escaping/numbers responding). Webb (1981) found no change in this fraction over the larval size range he examined (3-12 mm SL), indicating that changes in responsiveness alone were responsible for the decline in the vulnerability of northern anchovy larvae to *Amphiprion* with increasing larval length. In the present study, no significant trend existed in the success of avoidance movements over the size range of larvae studied by Webb (1981) but success of avoidance movements greatly increased in larger larvae (Fig. 5). The figure also indicates that northern anchovy larvae were much more successful in avoiding *Amphiprion* than in avoiding adult northern anchovy and that the larvae had the least success in avoiding chub mackerel.

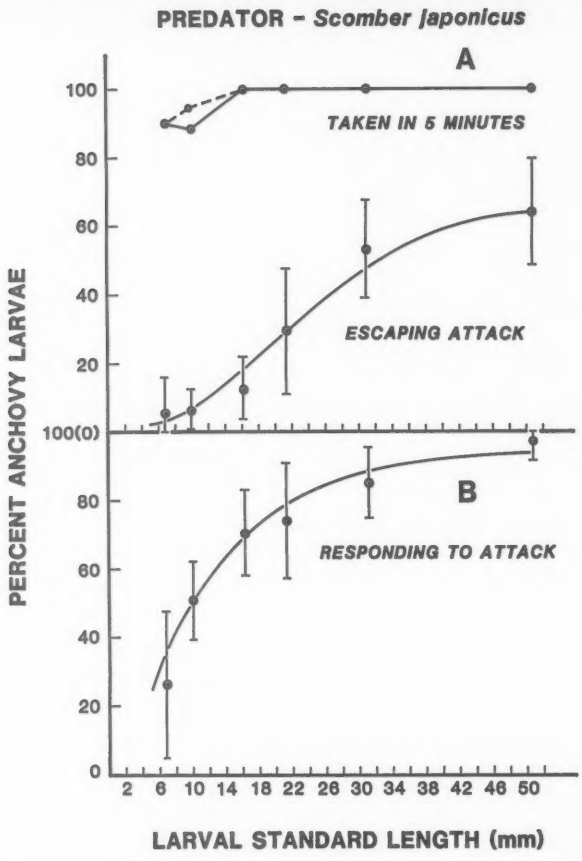

FIGURE 3.—Vulnerability of northern anchovy larvae and juveniles to juvenile chub mackerel predators as a function of anchovy length. A, percentage of northern anchovy larvae escaping attack; bars are 2 × SE; line is Weibull curve fit to six points using Marquardt's least squares method (Pielou 1981); equation is $N = K(1 - \exp(1 - (L/b) - \lambda))$ where $K = 0.66$, $b = 27.41$, N = percentage of larvae, L = larval length, and $\lambda = 2.12$; and predation rate of chub mackerel predators (percentage eaten in 5 min) where dashed line is data when experiments with biased predator feeding motivation are omitted. B, percentage of northern anchovy larvae that responded to the attack of a chub mackerel, bars are 2 × SE; and Weibull parameters for curve are $K = 0.93$, $b = 12.61$, and $\lambda = 1.24$.

Predation Rates

The predation rate of northern anchovy (proportion of larvae consumed by northern anchovy predators in 5 min) reached a maximum somewhere between larval lengths of 8.5 and 15 mm when all data were used, but it occurred between larval lengths of 8.5 and 11 mm when we deleted the experiment where northern anchovy predator performance was lower than average (dashed line in Figure 2A). Statistical comparisons of the fraction of larvae consumed in the various size classes indicated that 6.8 mm larvae were taken less often than larvae in 8.5, 11, and 15 mm size classes despite the fact that these larvae had a low escape ability ($P < 0.05$; normal approximation to the binomial mean; n = 35, 48, 40, and 60, for 5.9, 8.5, 11, and 15 mm size classes). Owing to their small size and

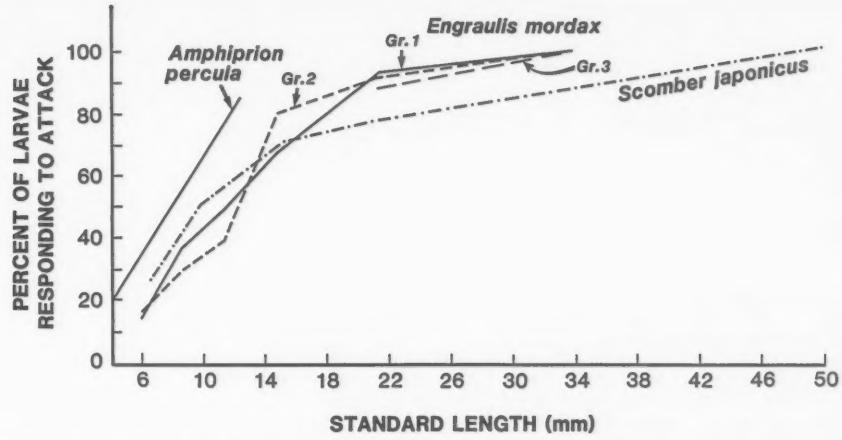

FIGURE 4.—Percentage of northern anchovy larvae that responded to attacks by adult northern anchovy (lines for the three different predator groups shown separately), chub mackerel and the aquarium fish *Amphiprion percula* (from Webb 1981).

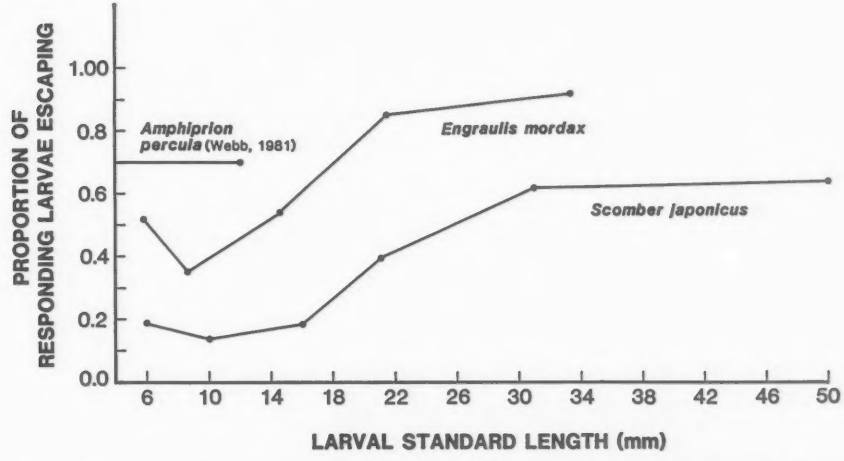

FIGURE 5.—The percentage of responding northern anchovy larvae in various length classes that escaped the predator. Species names identify the predator species.

lack of pigmentation, 6 mm larvae may have been less visible to the predators than larger larvae and consequently were detected less frequently. The decline in predation rates in larvae longer than 15 mm was the result of their greater escape ability.

The number of larvae consumed in 5 min was an insensitive measure of predation rates of chub mackerel, because they usually ate all larvae in the tank within 5 min regardless of their size. Only in the two smallest larval size groups (6-10 mm SL) were some larvae left after a 5-min elapsed time; the deletion of one experiment because of low chub mackerel predator performance changed the predation rate on 10 mm larvae from 87 to 95% (dashed line in Figure 3A). These adjusted data indicate that the feeding rate of chub mackerel was lowest when

the smallest larval size group (6.7 mm) were the prey.

Predator Behavior

Sighting distances, persistence of the attack, attack speed, and other characteristics of predator behavior were not well documented in our experiments because our focus was on the larvae. Such information could be quite useful if one were to develop a predation model for northern anchovy larvae, using northern anchovy or chub mackerel predators. We provide some general observations on the behavior of the predators.

Chub mackerel attacked 6.7 mm larvae from a shorter distance than larger larvae (t-test, $P = 0.05$), but no statistically significant trend was evident when northern anchovy were predators. Mean attack distances were a poor measure of sighting range as they included repeated, short-range attacks on the larger larvae. We observed both predator species swimming within 2-3 dm of the smallest larvae without attacking them, whereas larger larvae were always attacked from this distance indicating that sighting distances may be shorter for small larvae.

Adult northern anchovy usually attacked a larva only once during a feeding sequence, and if the larva escaped, it was rarely attacked again or pursued. On the other hand, if the chub mackerel did not capture the larva on the first attack, it usually turned and attacked again. Chub mackerel usually chased an escaping larva until it was captured. The attack speeds of adult northern anchovy, although not measured, seemed to be similar over a wide range of larval prey sizes, whereas the attack speeds of chub mackerel clearly were faster when attacking larvae greater than about 10 mm SL than when attacking smaller larvae.

DISCUSSION

Factors Affecting Larval Vulnerability

A low level of responsiveness seems to be the dominant feature of the vulnerability of northern anchovy larvae to fish predators over the smallest larval size classes we tested (6-10 mm SL). Presumably northern anchovy larvae <6 mm would respond even less frequently, as Webb (1981) found that only 9% of 2.9 mm northern anchovy larvae responded to the aquarium fish *Amphiprion percula*, whereas about 30% of 6 mm larvae did so. During this period vulnerability of northern anchovy larvae to fish predators seems to be primarily a function of visual detection by the predator, because when the larvae are detected they have a low probability of escaping. Our data on predation rates and maximum attack distances indicate that predation in the sea on the small, young larval stages might be lower than expected because of the short range at which such larvae may be detected. Thus, factors that affect the distance at which larvae are detected by predators, such as larval size, visual contrast, and water clarity (Vinyard and O'Brien 1976), may be the most important variables during the first 3 wk of life. As larvae grow they more often respond to the attacks of predators and escape them more frequently. Maturation of visual and lateral line systems (O'Connell 1981) may be the principal cause of this general increase in responsiveness with larval length. Although older larvae are more responsive, they are also more readily detected by predators because they are larger and have more pigmentation. Improved avoidance behavior may not completely compensate for the greater visibility of larvae in the 8-12 mm range, as our data on predation rates by northern anchovy indicated that the rates of consumption were highest for larvae in this range.

Larvae longer than 20 mm responded more frequently to northern anchovy than to chub mackerel predators, possibly because chub mackerel attacked such large larvae at much higher speeds. At higher attack speeds, less time is available for the larvae to respond; consequently, predators with the most rapid attack speeds evoke the lowest proportion of prey responses (Webb 1982). Thus one might expect a larva to respond to small fish predators more frequently than to larger ones, since attack speed would be expected to increase with predator size. This may explain why northern anchovy larvae (2.9-12 mm SL) responded more frequently to the small *Amphiprion* (44 mm) (Webb 1981) than they did to either northern anchovy or chub mackerel predators (Fig. 4). The pectoral swimming of *Amphiprion* might also provide more cues of an impending attack than did the swimming movements of either northern anchovy or chub mackerel.

In addition to size-specific avoidance capabilities and visibility, many other larval characteristics affect their vulnerability to predators. We briefly consider here three of these: effects of starvation, effects of the onset of schooling, and effects of variations in larval growth rates. Clupeoid larvae undergo degradation of muscle and other tissues during starvation, and a reduced predator avoidance behavior might be anticipated (Ehrlich 1974; O'Connell 1980). In a preliminary experiment Folkvord (1985)

reported that only 50% of starved, 33 mm northern anchovy larvae responded to the attacks of adult northern anchovy as compared with 100% for fed larvae. No starved 10 mm larvae escaped attack whereas 15-20% of the fed 10 mm larvae did so. The numbers of observations were insufficient for a statistical comparison, but recent work by Booman (unpubl. data, Southwest Fisheries Center, La Jolla, CA) indicates starvation can have a statistically significant effect on responsiveness of 10 mm northern anchovy larvae to adult northern anchovy predators.

The effect of the onset of larval schooling was not considered in these experiments; however, escape and response probabilities of individual larvae may not be altered greatly by the onset of schooling. The work of Major (1978) indicates that the most important effect of schooling may be to reduce the rate of attack by predators. He also found that the majority of Hawaiian anchovy captured by predators were isolated individuals that had moved away from the school, and predator success on schooled prey was similar to that on isolated prey. The onset of schooling in larval northern anchovy occurs between 11 and 15 mm SL, but the time spent in organized, cohesive schools increases throughout the northern anchovy's larval and juvenile periods (Hunter and Coyne 1982). Thus attack rates of predators might be expected to decline throughout later larval and juvenile life as the northern anchovy spends more time in cohesive schools. The onset of schooling occurs over the size range in which we observed the maximum predation rate (numbers consumed in 5 min) on individual northern anchovy larvae by northern anchovy predators. Thus predation pressure may be an important evolutionary factor in the timing of the onset of schooling during the larval stage.

The interaction between larval growth rate and size-specific vulnerability to predation may be an important source of interannual variation in larval mortality (Shepherd and Cushing 1980; Smith 1985). A simple calculation illustrates this point using the size-specific vulnerability of northern anchovy larvae (10-20 mm SL) to adult northern anchovy predators. We assumed larval escape ability to be an inverse measure of predator vulnerability and normalized it to the average mortality rate over this size interval (Table 1). Thus in our calculation, the rate larval mortality decreased with increasing larval size was inversely proportional to the rate escape ability increased with size (larval escape ability increased linearly with larval length over the 10-20 mm length range). Our calculation indicated that a 50% increase in growth rate from the average rate of growth in the sea resulted in a 58% increase in survival in 30 d compared with average conditions. Decreasing the growth rate by 50% gave a 37% decrease in survival over the same interval. A longer period of reduced or enhanced growth rates will, of course, give a larger deviation from average survival values.

TABLE 1.—Calculation of the effect of growth rate on survival of 10-20 mm northern anchovy larvae when mortality is inversely proportional to length specific escape probabilities.

Terms	Parameter values
Z = mortality rate	Z = 0.05 at 16 mm[a]
S = larval length (mm)	10 mm < S < 20 mm
G = growth rate	G = 0.325 mm/d[b]
T = time	T = 30 d
N = relative numbers of larvae	$N(0)$ = 1

Initial equations

$$Z = 0.15 - (0.00625 \times S)$$ [a]

$$S = 10 + (G \times T)$$

$$dN/dt = -(Z \times N)$$

Final equations after substitution and integration

$$N = 0.0724 \times \exp(2.808 \times G)$$

Estimates of survival after 30 days

Growing conditions	Growth rate (mm/d)	Relative numbers of larvae	Relative survival (%)
Average	0.325	0.1803	—
50% increase	0.488	0.2850	+58
50% decrease	0.162	0.1141	−37

[a]Mortality function generated from larval anchovy escape data with adult northern anchovy as predators. Values are normalized to Z 0.05 at 16 mm (Smith 1985).
[b]From Smith (1985), 0.325 ± 50% also used in calculation.

Effect of Predator Size

We examined the existing literature on predators of larval northern anchovies to determine how the ability to escape a predator varied among different predator species. Regardless of the predator species, larval escape ability always increases with larval size, but the rates vary greatly with predator size. In general the smaller the predator, the faster larval escape abilities improve with increasing larval length (Fig. 6). The results of our work on *E. mordax* were similar to those of Brownell (1985) on *E. capensis*. However, capture success of the 85 mm *E. mordax* predators used in our study was about 20% higher than the 34 mm *E. capensis* predators used by Brownell.

The extent of the predator field for a given size and species of predator can be defined as the larval size range in which larval escape success is <100%. For adult northern anchovy predators (85 mm and

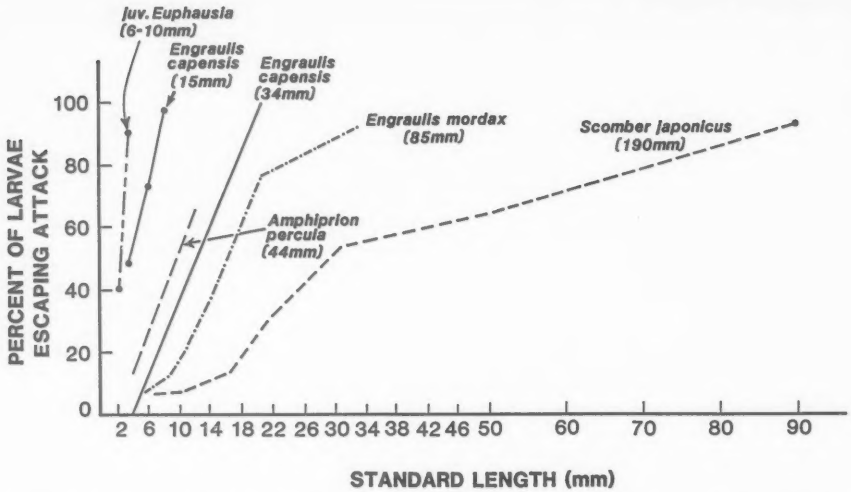

FIGURE 6.—Percentage of larval and juvenile anchovies escaping attacks of various predators as a function of length. Data for *Engraulis capensis* feeding on larval *E. capensis* are from Brownell (1984); juvenile *Euphausia* fed *E. mordax* from Theilacker and Lasker (1974); *Amphiprion percula* fed *E. mordax* from Webb (1981); and others are from this study. Numbers indicate length (mm) of the various predators.

larger), the field extends from the egg (Hunter and Kimbrell 1980) to about 40 mm. The field for juvenile chub mackerel is much wider than that for northern anchovy extending from northern anchovy eggs to adults (120 mm), whereas the predation field for *Euphausia* is restricted to the yolk-sac period (Theilacker and Lasker 1974). The limited data available (Table 2) provide a crude index for the upper limit of the predator field for northern anchovy larvae. When the larval length exceeds about 50% of the predator length little or no predation occurs.

TABLE 2.—Upper limit of some predator fields for larval anchovies, *Engraulis mordax* and *E. capensis*.

Predator		Upper limit of predator field[1]	
Species	Predator length (mm)	Larval length (mm)	Larval length / Predator length
Euphausia juveniles (Theilacker and Lasker 1974)	8	4.5	0.6
Engraulis capensis (Brownell 1984)	15	8.2	0.6
Engraulis capensis (Brownell 1984)	34	20	0.6
Amphiprion percula (Webb 1981)	44	18	0.4
Engraulis mordax (this study)	85	[2]~40	0.5
Scomber japonicus (this study)	190	[2]~120	0.6

[1]Upper limit = larval size at which all larvae escape predator.
[2]Extrapolated values.

CONCLUSIONS

Much of the past research on recruitment has focused on early larval stages where mortality rates are the highest (May 1974). Our work supports a growing contention that later larval stages and early juvenile stages may be as important in determining year-class strength (Smith 1985) and that such effects might be mediated through an interaction between larval growth and size-specific vulnerability to predators. Our results and those of others indicate that the ability of northern anchovy larvae to escape pelagic predators increases throughout the larval stage. On the other hand, the susceptibility of larvae to predation may not decrease strictly according to size because large larvae may be more easily detected by visual feeding planktivorous fishes than smaller ones.

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LITERATURE CITED

BAXTER, J. L.
1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. CalCOFI Rep. 11:110-116.

BROWNELL, C. L.
1985. Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. Trans. Am. Fish. Soc. 114:512-518.

CURIO, E.
1976. The ethology of predation. Springer-Verlag, N.Y., 249 p.

EHRLICH, K. F.
1974. Chemical changes during growth and starvation of herring larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 310-323. Springer-Verlag, N.Y.

FRANK, K. T., AND W. C. LEGGETT.
1984. Selective exploitation of capelin (*Mallotus villosus*) eggs by winter flounder (*Pseudopleuronectes americanus*): capelin egg mortality rates, and contribution of egg energy to the annual growth of flounder. Can. J. Fish. Aquat. Sci. 41:1294-1302.

FOLKVORD, A.
1985. Size specific vulnerability of northern anchovy *Engraulis mordax* larvae to predation by fishes. MS Thesis, University of California at San Diego, 96 p.

HEWITT, R. P., G. H. THEILACKER, AND N. C. H. LO.
1985. Causes of mortality in young jack mackerel. Mar. Ecol. Ser. 26:1-10.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
1984. Inferences regarding predation on the early life stages of cod and other fishes. Fløddevigen rapportser., 1. ISSN 0333-2594 The propagation of cod *Gadus morhua L*, p. 533-562.

HUNTER, J. R., AND K. M. COYNE.
1982. The onset of schooling in northern anchovy larvae, *Engraulis mordax*. CalCOFI Rep. 23:246-251.

HUNTER, J. R., AND C. A. KIMBRELL.
1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 78:811-816.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MAJOR, P. F.
1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Anim. Behav. 26:760-777.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

MÖLLER, H.
1984. The reduction of a larval herring population by jellyfish predator. Science 224:621-622.

O'CONNELL, C. P.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-484.
1981. Development of organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. Am. Zool. 21:429-446.

PIELOU, E. C.
1981. The usefulness of ecological models: a stock-taking. Q. Rev. Biol. 56:17-31.

PURCELL, J. E.
1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci. 37:739-755.

SCHAEFER, K. M.
1980. Synopsis of data on the chub mackerel, *Scomber japonicus*, 1782, in the Pacific Ocean. *In* W. H. Bayliff (editor), Synopses of biological data on eight species of scombrids. Inter-Am. Trop. Tuna Comm., Spec. Rep. 2, p. 395-445.

SHEPHERD, J., AND D. H. CUSHING.
1980. A mechanism for density dependent survival of larval fish as the basis of stock recruitment relationship. J. Cons. int. Mer 39:160-167.

SMITH, P. E.
1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):69-82.

THEILACKER, G. H.
1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull., U.S. 84: 1-15.

THEILACKER, G. H., AND R. LASKER.
1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 287-299. Springer Verlag, N.Y.

VAN DER VEER, H. W.
1985. Impact of coelenterate predation on larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* in the western Wadden Sea. Mar. Ecol. Prog. Ser. 25:229-238.

VINYAND, G. L., AND W. J. O'BRIAN.
1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33:2845-2849.

WEBB, P. W.
1981. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. Fish. Bull., U.S. 79:727-735.
1982. Avoidance responses of fathead minnow to strikes by four teleost predators. J. Comp. Physiol. 147:371-378.

OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF THE COWNOSE RAY, *RHINOPTERA BONASUS*, IN CHESAPEAKE BAY[1,2]

JOSEPH W. SMITH AND JOHN V. MERRINER[3]

ABSTRACT

Cownose rays, *Rhinoptera bonasus*, are abundant in Chesapeake Bay during summer. We made observations on the reproductive biology of specimens collected primarily from commercial pound nets and haul seines from May through October 1976-78. Clasper development suggested that males began to mature at disc widths (DW) of 75-85 cm. Males judged as mature averaged about 90 cm DW. Macroscopic inspection of the oviducts suggested that females began to mature at 85-92 cm DW. Females judged as mature averaged 96 cm DW. Only the left reproductive tract in female cownose rays appeared functional and only one embryo per gravid female was observed. A total of 67 embryos ranging 18-440 mm DW were collected and the sex ratio of the embryos was 1:1. Gravid females carried three-quarter term embryos in May and parturition occurred in late June and July. Full-term embryos averaged about 40 cm DW. Gestation of another group of embryos began by August. Growth of these embryos was rapid and they were relatively large when cownose rays left the Chesapeake Bay in October. Cownose rays exhibited aplacental viviparity. Yolk reserves supplied the initial energy demands of the embryos (up to about 20 cm DW), but histotrophic secretions of uterine villi provided nutrition for the young through the remainder of gestation.

The cownose ray, *Rhinoptera bonasus*, a large myliobatoid ray, which attains a maximum weight of 23 kg, is abundant in Chesapeake Bay during summer (Schwartz 1965; Musick 1972) where it preys heavily on commercially important shellfish (Merriner and Smith 1979). Because of the severe damage to shellfish beds and the paucity of information on the biology of the cownose ray, the Virginia Institute of Marine Science began a study on the life history of the cownose ray in 1976. Prior to our work, information on the cownose ray's reproductive biology was primarily limited to observations of single gravid females, usually included in more general literature (Gudger 1910; Bigelow and Schroeder 1953; Joseph 1961; Hoese 1962; Bearden 1965; Orth 1975), and size at maturity was unknown (Bigelow and Schroeder 1953). Schwartz's (1967) brief abstract represented the most complete statement on the species' reproductive cycle. Here, we report on the reproductive biology of the cownose ray, specifically on 1) the estimated size at maturity for both sexes, 2) the definition of the gestation period, and 3) the description of the embryonic development.

MATERIALS AND METHODS

Most cownose rays were taken from pound nets in the lower Chesapeake Bay during three summers, 1976-78, but some rays came from haul seines used in spring along the Virginia-North Carolina coast, and from gill nets and rod and reel catches. Disc width (DW = distance between tips of the pectoral fins) was measured in mm on a measuring board. References to specimen size (including embryos) hereafter are disc width measurements.

We judged male cownose rays sexually mature if 1) the clasper rhipidion was fully developed and easily spread and 2) clasper cartilages were well calcified (rigid). We measured clasper length as the distance from the junction of the clasper and pelvic fin to the distal end of the clasper. Criteria modified from Smith (1975) were used to determine the following stages of sexual maturity for females:

1) immature - ovaries thin and flaccid; uterus thin and elongate, lining appears rugous.

2) maturing - ovary slightly developed, yellowish ova visible, ova <1 cm diameter; uterus somewhat dilated, trophonemata (uterine villi) small, generally <0.5 cm long.

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3) mature - ovary with large yellowish ova >1 cm diameter; uterus well-developed and rich in trophonemata, generally >1 cm long.

Uteri and oviducts were opened and inspected for ova or embryos. Embryos were weighed and measured for disc width (mm). Yolk-sac volume (mL) was measured by volumetric displacement in a graduated cylinder.

RESULTS AND DISCUSSION

Like many other elasmobranch populations which occur along the east coast of the United States, cownose rays are highly migratory and exhibit a northward coastal migration in spring and a southward movement in fall (Schwartz 1965; Smith 1980). Our earliest spring collection of adult rays occurred during 2-5 May 1977 on the North Carolina Outer Banks. Our latest fall collection of adult males was on 7 September 1978 in the lower York River, while the latest fall collection of adult females occurred on 12 October 1977 near Cape Henry, VA, at the mouth of the Chesapeake Bay. Adult rays were absent from pound net catches in the lower bay after mid-October; furthermore, they were unavailable to us until the following spring when they migrated back into Chesapeake Bay.

Size at Maturity

At the onset of sexual maturity, terminal cartilage elements develop distally on the claspers of male elasmobranchs (Bigelow and Schroeder 1953), and the allometric growth of these appendages has been used to determine the attainment of sexual maturity in various elasmobranchs (e.g., Clark and Von Schmidt 1965; Struhsaker 1969; Gilbert and Heath 1972). In male cownose rays the ratio of clasper length to disc width increases slightly at 75-85 cm DW suggesting the onset of sexual maturity (Fig. 1). Males <75 cm (n = 68) appear immature; their testes are thin, white and ribbonlike and their claspers are narrow and flexible. Males ranging 80-98 cm ($\bar{x}$ = 89.8 cm; n = 115) appear mature; their testes are pinkish white in color and greatly swollen, and their claspers are rigid and well-calcified. Based on clasper length to disc width ratio and cursory observations of the testes, we estimated that male cownose rays begin sexual maturation at about 80 cm and most are probably mature at disc widths >84 cm.

Considerable discrepancies exist in the literature concerning size of female cownose rays at sexual maturity. Gudger (1910) claimed a female about 60 cm wide gave birth to a pair of young. Bearden (1965) reported four premature young from a female measuring 712 mm (disc width?) taken in South Carolina. Joseph (1961) and Orth (1975) collected gravid females in Chesapeake Bay of 89 and 90 cm, respectively. We classified females <84 cm (n = 86) as immature (immature ovaries are thin and flaccid, and immature uteri are thin and elongate). Females that we judged as mature ranged 84.5-100 cm ($\bar{x}$ = 96 cm; n = 117). Mature ovaries possess yellowish ova >1 cm in diameter; the left uterus of mature females is well-developed and rich in trophonemata (uterine villi), which are generally >1 cm long, red in color, and spatulate distally. We classified eight specimens (range: 84-92 cm) as maturing females. Although ova <1 cm in diameter are visible in the ovary, the left uterus is not well-developed and the trophonemata are generally <0.5 cm long. The smallest gravid female measured 87 cm. Based on these observations we estimated that female cownose rays begin sexual maturation at 85-90 cm and are mature at disc widths >90 cm.

Only the left reproductive tract appears functional in female cownose rays. There is no macroscopic evidence of follicular development in the right ovary. The right uterus in mature specimens shows some distension (ca. 3 cm wide), but does not exceed the breadth of the left uterus. Embryos and ova occur only in the left uterus, although we found an empty shell capsule in the right uterus of several gravid females. Nonfunctional right reproductive tracts have been reported in the roughtail stingray, *Dasyatis centroura*, (Struhsaker 1969) and the bluntnose stingray, *D. sayi* (Gudger 1912; Hamilton and Smith 1941; Hess 1959).

Reproductive Cycle

Numerous literature accounts reported on the capture of singular gravid cownose rays (Smith 1907; Gudger 1910; Bigelow and Schroeder 1953; Joesph 1961; Hoese 1962; Bearden 1965; Orth 1975) and these provided fragmentary information on the ray's gestation cycle. Schwartz's (1967) abstract defined June through October as the breeding cycle and closely parallels our results, although we disagreed on size at parturition. We collected 67 embryos (range: 18-440 mm; sex undetermined for 3 specimens) from the lower Chesapeake Bay and vicinity. Data for 19 embryos (all specimens sexed, length undetermined for 8 specimens) taken in April 1978 near Cape Lookout, NC, were provided to us by W.

S. Otwell[4] (Fig. 2). Only one embryo per gravid female was observed. The overall sex ratio of embryos (40♂:43♀) did not differ significantly from 1:1.

Gravid female rays migrate into Chesapeake Bay in spring with well-developed embryos that we designated as approximately three-quarter term.

[4]W. S. Otwell, formerly of North Carolina State University Food Science Laboratory, Morehead City, NC; presently at University of Florida, Food Science Department, Gainesville, FL 32611, pers. commun. April and May 1978.

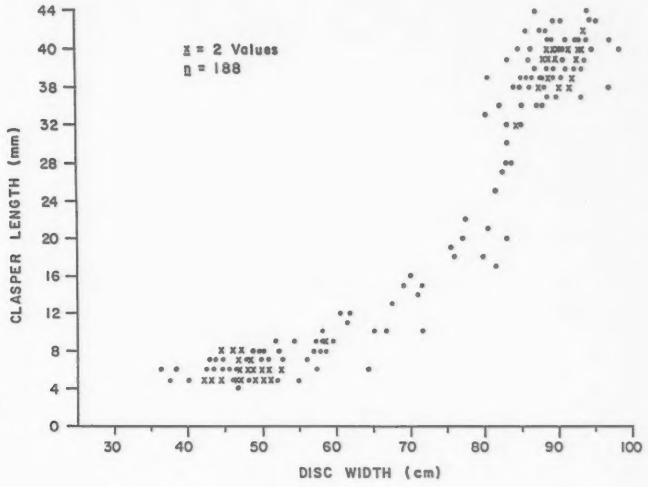

FIGURE 1.—Relationship of clasper length (mm) to disc width (cm) for 188 male *Rhinoptera bonasus*.

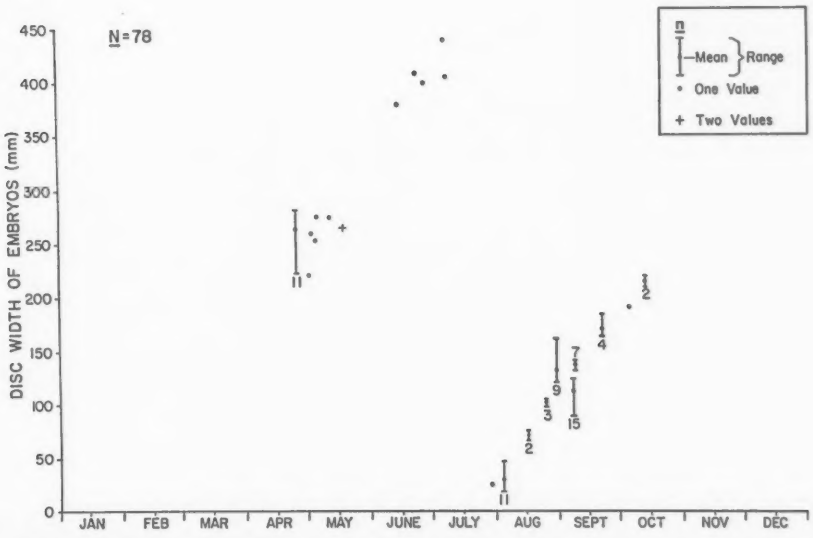

FIGURE 2.—Relationship of disc width (mm) to date of capture for *Rhinoptera bonasus* embryos collected 1976 through 1978.

Embryos collected in early May on the Outer Banks and in the lower York River average 259 mm (range: 221-276 mm; n = 7), and those collected from Cape Lookout, NC, in mid-April (Otwell fn. 4) average 264 mm (range: 222-281 mm; n = 11) (Fig. 2). By late June and early July the embryos are full term ($\bar{x}$ = 413 mm; n = 4). Parturition occurs at this time and the first free-swimming young appear in pound net catches. Embryo weight gain in spring is noteworthy; three-quarter term embryos in April and May average 310 g (range: 192-392 g; n = 16), while the weight of full-term individuals in late June increases fourfold averaging 1,291 g (range: 1,134-1,409 g; n = 3). Schwartz (1967) reported that term individuals average 305 mm DW, however, embryos we considered full term are considerably larger (ca. 400 mm) and the smallest free-swimming ray we collected was 323 mm. Perhaps, the embryos Schwartz (1967) considered full term were taken in early June and were not yet ready for parturition.

Female rays ovulate following parturition. We found encapsulated uterine eggs in specimens taken on 28 June and 21 July. In early August the embryos are 20-30 mm wide and have lost the shell capsule. By late August they average 125 mm (Figs. 2, 3). When adult rays leave the Chesapeake Bay in late September and early October, the embryos are relatively large, up to 220 mm.

Reproductive cycles of large elasmobranchs are often difficult to describe because during certain stages of pregnancy, individuals may be inaccessible as a result of schooling and migratory behavior (Holden 1974). Since cownose rays leave Chesapeake Bay by November and do not return until May, we could not determine precisely the length of gestation. Nevertheless, an 11-12 mo gestion period seems most probable. Within this context, the rapid embryonic growth observed in summer would slow during winter. A slowdown or cessation of intrauterine growth would be expected if gravid females experience high energy demands during an extensive migration to distant wintering grounds, possibly northern South America as suggested by Schwartz (1965). Thus, the embryos from late summer and fall

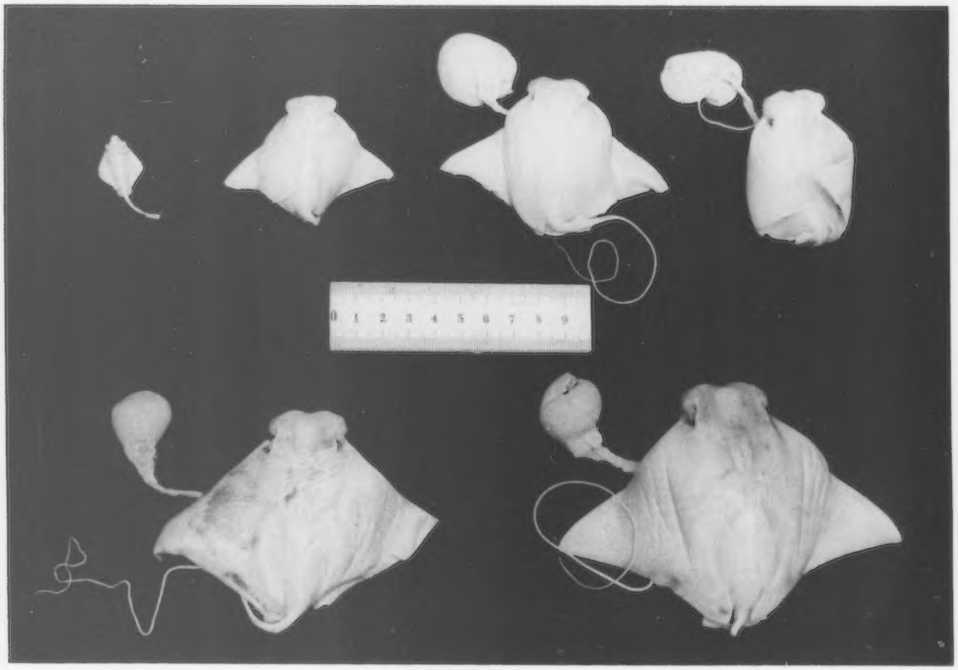

FIGURE 3.—Series of *Rhinoptera bonasus* embryos ranging from 18 to 140 mm disc width collected in late summer and fall.

would be born the following summer when the adults return to Chesapeake Bay, a gestation period of 11-12 mo beginning in July or August and ending in June or July.

The relatively large size of cownose ray embryos in late September and early October suggests the possibility of two 5-6 mo gestation periods. Parturition might occur on the cownose rays' wintering grounds followed by the gestation of another brood of embryos destined for birth the following summer. This hypothesis is not unprecedented, since the presence of well-developed young in the spiny butterfly ray, *Gymnura altavela*, during May in Delaware Bay and during February off the coast of North Carolina (27 fathoms) led Daiber and Booth (1960) to propose two 5-6 mo gestation periods per year for this species. Precise definition of the cownose ray gestation cycle will require collecting gravid female rays on their wintering grounds.

Embryonic Development and Nutrition

The shell capsule of the cownose ray, which we observed twice in utero, is of a greenish amber, thin diaphanous material, and is about 10 cm long. One capsule held a single ovum, while the capsule from a second female contained three ova. Ova are yellow, extremely flaccid, and about 3-4 cm in diameter.

The embryos in late summer and fall possess yolk stalks and yolk sacs, although these often become detached during collection (Fig. 3). The smallest embryos we collected are about 20 mm wide, batoid in appearance, and unencapsulated. Numerous external branchial filaments (ca. 15-30 mm long), which emerge from the gill slits, are highly conspicuous on small embryos (18-75 mm). These filaments are absent in embryos larger than 89 mm.

Three-quarter term embryos are upright in the uterus (ventral surface of the embryo on the ventral wall of the uterus) with the rostrum pointed forward. The pectoral fins are folded dorsally. The tail and heavily sheathed spine are bent forward along the dorsum of the disc. The yolk sac and stalk are almost completely absorbed; only about 3 mm of the umbilicus protrudes from the abdomen.

Full-term embryos are similarly oriented. However, the umbilicus is completely absorbed, leaving only a small scar that is evident on free-swimming young. Pigmentation is that of the adults, i.e., chocolate-brown dorsally, white ventrally, and black caudally. Several tooth plates were discovered in the left uterus from which a full-term young was removed, confirming Bigelow and Schroeders' (1953) report that tooth replacement begins in utero.

During the early stages of gestation the uterus is rigid and thick-walled, but it gradually expands to accommodate the developing young. Just prior to parturition, it is extremely distended (ca. 15 cm at its greatest breadth), thin-walled, and flaccid.

Myliobatoids overcome spatial restrictions in utero by rolling the pectoral fins dorsally or ventrally, along the anterioposterior axis (Gudger 1951), and some studies report that larger than average females carry more and larger offspring (e.g., Babel 1967). Although we observed multiple encapsulated ova in cownose rays, and others have cited the occurrence of multiple embryos in utero (Smith 1907; Gudger 1910; Bearden 1965), we never found more than one embryo per gravid female. Setna and Sarangdhar (1949) and James (1962, 1970) made similar observations for the Javanese cownose ray, *R. javanica*, from the Indian Ocean. Our data for term embryos (n = 4) are insufficient to corrolate embryo size with parent's size; however, we suspect that in general only one cownose ray embryo is carried to term.

Embryonic nutrition is from yolk and histotrophe. Yolk of the late summer and fall embryos (n = 33) gradually diminishes between August and October (Fig. 4), and most yolk reserves are probably utilized when embryos are about 20 cm. Histotrophe, a viscid, yellowish secretion of the uterus (as also cited by Schwartz 1967), also nourishes the embryos. The amount of histotrophe, although not quantified, increases considerably as gestation progresses. Trophonemata, the uterine villi that produce histotrophe, are deep red, flattened in cross section and spatulate distally. They attain their greatest length (ca. 2-3 cm) in females with near full-term embryos. The trophonemata occasionally invade the gill slits.

In summarizing chondrichthyan, fetal-maternal relationships, Wourms (1977) noted that the efficiency of placental analogues, the villiform trophonemata, far surpasses that of the yolk-sac placenta exhibited by some carcharhinids. In cownose ray embryos, yolk apparently provides initial nutritional requirements. Embryos may augment yolk supplies during the first month of gestation by absorbing histotrophe via the external branchial filaments, as was suggested for *Urolophus halleri* by Babel (1967). After October, histotrophe supplies nourishment for the remainder of the gestation period, probably engulfed via the mouth, spiracles, and gill slits.

Viviparity and the use of nursery areas that are relatively free of predators, e.g., Chesapeake Bay, no doubt protect young cownose rays. Large carcharhinids, of which batoids are purported to be a

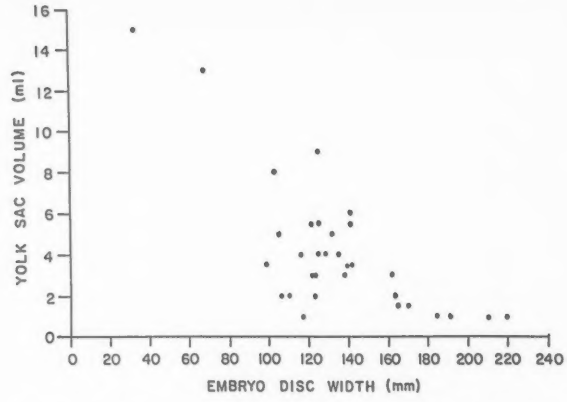

FIGURE 4.—Relationship of yolk-sac volume (mL) to disc width (mm) for *Rhinoptera bonasus* embryos collected in late summer and fall.

favorite prey (Darnell 1958; Budker 1971) are abundant seaward of the Virginia capes during summer (Lawler 1976), but generally only the sandbar shark, *Carcharhinus plumbeus*, and the bull shark, *C. leucas*, frequent the Chesapeake Bay proper (Schwartz 1960; Musick 1972). Although gravid female sandbar sharks utilize the eastern shore of the Chesapeake Bay (Lawler 1976), they may not pose a threat to cownose rays, since the female sandbar sharks generally abstain from feeding while on their pupping grounds and males tend to avoid such areas (Springer 1960). Bull sharks (Schwartz 1959) may represent the only major predators of rays in Chesapeake Bay during summer.

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LITERATURE CITED

BABEL, J. S.
1967. Reproduction, life history, and ecology of the round stingray, *Urolophus halleri* Cooper. Calif. Dep. Fish Game, Fish Bull. 137:1-104.

BEARDEN, C. M.
1965. Elasmobranch fishes of South Carolina. Contrib. Bears Bluff Lab. 42:1-19.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Western North Atlantic. Pt. 2. Sawfishes, guitarfishes, skates, rays, and chimaeroids. Mem. Sears Found. Mar. Res., Yale Univ. 1:1-588.

BUDKER, P.
1971. The life of sharks. Columbia Univ. Press, N.Y., 222 p.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf Coast of Florida. Bull. Mar. Sci. 15:13-83.

DAIBER, F. C., AND R. A. BOOTH.
1960. Notes on the biology of the butterfly rays, *Gymnura altavela* and *Gymnura micrura*. Copeia 1960:137-139.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci. Univ. Tex. 5:353-416.

GILBERT, P. W., AND G. W. HEATH.
1972. The clasper-siphon sac mechanism in *Squalus acanthias* and *Mustelus canis*. Comp. Biochem. Physiol. A Comp. Physiol. 42:97-119.

GUDGER, E. W.
1910. Notes on some Beaufort fishes-1909. Am. Nat. 44: 395-403.
1912. Natural history notes on some Beaufort, N.C., fishes, 1910-11. No. I. Elasmobranchii—with special reference to utero-gestation. Proc. Biol. Soc. Wash. 25:141-156.

1951. How difficult parturition in certain viviparous sharks and rays is overcome. J. Elisha Mitchell Sci. Soc. 67:56-86.

HAMILTON, W. J., JR., AND R. A. SMITH.
1941. Notes on the sting-ray, *Dasyatis say* (LeSueur). Copeia 1941:175.

HESS, P. W.
1959. The biology of two sting rays, *Dasyatis centroura* Mitchill 1815 and *Dasyatis say* Lesueur 1871, in Delaware Bay. M.S. Thesis, Univ. Delaware, Newark, 42. p.

HOESE, H. D.
1962. Sharks and rays of Virginia's seaside bays. Chesapeake Sci. 3:166-172.

HOLDEN, M. J.
1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* F. R. Harden-Jones (editor), Sea fisheries research, p. 117-137. Wiley, N.Y.

JAMES, P. S. B. R.
1962. Observations on shoals of the javanese cownose ray *Rhinoptera javanica* Müller and Henle from the Gulf of Mannar with additional notes on the species. J. Mar. Biol. Assoc. India 4:217-223.
1970. Further observations on shoals of the javanese cownose ray *Rhinoptera javanica* Müller and Henle from the Gulf of Mannar with a note on the teeth structure in the species. J. Mar. Biol. Assoc. India 12:151-157.

JOSEPH, E. B.
1961. An albino cownose ray, *Rhinoptera bonasus* (Mitchill) from Chesapeake Bay. Copeia 1961:482-483.

LAWLER, E. F.
1976. The biology of the sandbar shark *Carcharhinus plumbeus* (Nardo, 1827) in the lower Chesapeake Bay and adjacent waters. M.A. Thesis, College of William and Mary, Williamsburg, 48 p.

MERRINER, J. V., AND J. W. SMITH.
1979. A report to the oyster industry of Virginia on the biology and management of the cownose ray (*Rhinoptera bonasus*, Mitchill) in lower Chesapeake Bay. Spec. Rep. Appl. Mar. Sci. Ocean Eng. 216, 33 p. Va. Inst. Mar. Sci.

MUSICK, J. A.
1972. Fishes of Chesapeake Bay and the adjacent coastal plain. *In* M. L. Wass (editor), A check list of the biota of lower Chesapeake Bay, p. 175-212. Va. Inst. Mar. Sci., Spec. Rep. No. 65.

ORTH, R. J.
1975. Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. Chesapeake Sci. 16:205-208.

SCHWARTZ, F. J.
1959. Two eight-foot cub sharks, *Carcharhinus leucas* (Müller and Henle), captured in Chesapeake Bay, Maryland. Copeia 1959:251-252.
1960. Additional comments on adult bull sharks, *Carcharhinus leucas* (Müller and Henle), from Chesapeake Bay, Maryland. Chesapeake Sci. 1:68-71.
1965. Inter-American migrations and systematics of the western Atlantic cownose ray, *Rhinoptera bonasus*. [Abstr.] Meet. Assoc. Isl. Mar. Lab. Caribb., 1 p. 6th Meet., Isla Margarita, Venez. 20-22 Jan.
1967. Embryology and feeding behavior of the Atlantic cownose ray *Rhinoptera bonasus*. [Abstr.] Meet. Assoc. Isl. Mar. Labs. Carib. 1 p. 7th Meet., Barbados, W.I., 24-26 Aug.

SETNA, S. B., AND P. N. SARANGDHAR.
1949. Breeding habits of Bombay elasmobranchs. Rec. Indian Mus. (Calcutta) 47:107-124.

SMITH, H. M.
1907. The fishes of North Carolina. N.C. Geol. Econ. Surv. 2:47.

SMITH, J. W.
1980. The life history of the cownose ray, *Rhinoptera bonasus* (Mitchill 1815), in lower Chesapeake Bay, with notes on the management of the species. M.A. Thesis, College of William and Mary, Williamsburg, 151 p.

SMITH, M. S.
1975. *A. P. Knight* Groundfish Cruise No. 74-2, October 15-17, 1974 (Data Record). Fish. Res. Board Can. Manuscr. Rep. Ser. No. 1336, 13 p.

SPRINGER, S.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61:1-38.

STRUHSAKER, P.
1969. Observations on the biology and distribution of the thorny stingray, *Dasyatis centroura* (Pisces:Dasyatidae). Bull. Mar. Sci. 19:456-481.

WOURMS, J. P.
1977. Reproduction and development in chondrichthyan fishes. Am. Zool. 17:379-410.

NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SPAWNING IN SAN FRANCISCO BAY, CALIFORNIA, 1978-79, RELATIVE TO HYDROGRAPHY AND ZOOPLANKTON PREY OF ADULTS AND LARVAE

MICHAEL F. MCGOWAN[1]

ABSTRACT

Eggs and larvae of *Engraulis mordax* were sampled by nets monthly for one year. Either eggs or larvae were caught every month. Both were most abundant when water temperature was high. Mean egg abundance did not differ among stations but larvae were more abundant within the San Francisco Bay at high and low salinity than near the ocean entrance to the Bay. Larvae longer than 15 mm were collected over the shoals in spring and autumn but were in the channel during winter. Zooplankton and microzooplankton were abundant relative to mean California Current densities. Adult spawning biomass in the Bay was 767 tons in July 1978, based on egg abundance and fecundity parameters of oceanic animals. San Francisco Bay was a good spawning area for northern anchovy because food for adults and larvae was abundant and because advective losses of larvae would have been lower in the Bay than in coastal waters at the same latitude.

The northern anchovy, *Engraulis mordax*, is the most abundant fish in San Francisco Bay (Aplin 1967), but little is known about the seasonal duration or areal extent of northern anchovy spawning there (Eldridge 1977; Sitts and Knight 1979; Wang 1981). In the California Current, spawning is thought to be related to abundance of food for adults (Brewer 1978) or to seasonal patterns of abundance of food for larvae (Lasker 1978). Dense patches of appropriate food for larvae are believed to be necessary for survival of larvae (Lasker 1975; Scura and Jerde 1977). Zooplankton are generally more abundant in estuaries than in coastal and oceanic waters. Therefore, San Francisco Bay, the largest estuary on the west coast of North America, could be a favorable habitat for spawning northern anchovy and their developing larvae.

The northern anchovy could affect plankton dynamics in the San Francisco Bay (the Bay) by preying on zooplankton and by excreting concentrated nutrients for phytoplankton. It is the target of a seasonal bait fishery (Smith and Kato 1979), and it is an important forage fish for many other species (Recksiek and Frey 1978). Quantitative estimates of the adult stock size and numbers of eggs and larvae are needed to understand the ecology of this anchovy in the Bay.

This paper reports the results of a 1-yr survey of the northern anchovy eggs and larvae, zooplankton, and microzooplankton in San Francisco Bay. Distribution and abundance of eggs and larvae were related to water temperature, salinity, turbidity, stratification, abundances of potential adult prey, and potential larvae prey. The suitability of the Bay for spawning and development of larvae was assessed. An estimate of spawning stock abundance within the Bay was calculated from egg abundance, and the impact of this biomass of anchovies on the zooplankton was estimated.

MATERIALS AND METHODS

Study Site

San Francisco Bay consists of three major parts (Fig. 1): 1) Central Bay opens to the Pacific Ocean through the Golden Gate at lat. 37°49′N, long. 112°29′W; 2) North Bay receives the drainage from the Sacramento and San Joaquin Rivers and includes Suisun, San Pablo, and Richardson Bays; 3) South Bay is the largest single embayment, extending some 27 nmi from Coyote Creek in the south to the Oakland-San Francisco Bay Bridge in the north. The following description of San Francisco Bay was taken from Conomos and Peterson (1977). Mean depth is 6 m at mean lower low water, or 2 m if the large expanses of mudflats are included. There is a 10 m deep dredged ship channel in the northern part. Tides are mixed semidiurnal ranging from 1.7 m at the Golden Gate to 2.7 m at the south-

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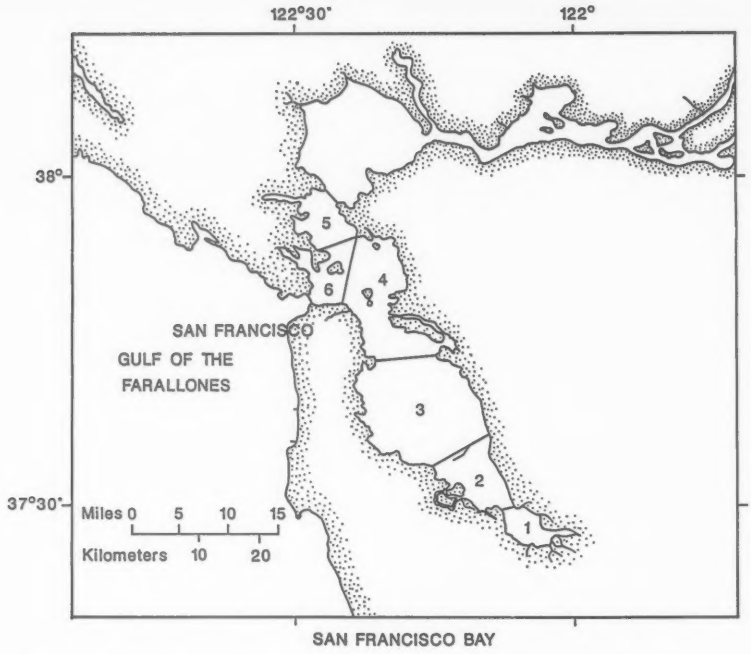


FIGURE 1.—Locations of stations and the areas represented by each station sampled monthly May 1978-April 1979.

ern end of South Bay. The tidal prism is 27% of the Bay volume. Maximum tidal currents occur in the channels and may be 225 cm/s (4.5 kn) at the Golden Gate. More than 90% of the freshwater entering San Francisco Bay enters North Bay from the Sacramento and San Joaquin Rivers. Less than 10% enters South Bay from small tributary streams and sewage. Because of the difference in freshwater inflow the northern and southern reaches are very different types of estuary. North Bay is partially-to-well-mixed with true two-layer estuarine circulation. South Bay, dependent for water exchange on tidal circulation and occasional incursions of freshwater from the north during wet winters, resembles a coastal lagoon.

The heterogeneous nature of San Francisco Bay requires that stations be representative of the diverse areas of the Bay. The stations (Fig. 1) were located in the channel adjacent to the shoals in the South Bay in 5-6 m of water (stations 1 and 2); just north of San Bruno Shoal in 3 m of water (station 3); east of Treasure Island over a dredge borrow pit in 10 m of water (station 4); in midchannel just south of the Richmond-San Rafael Bridge in 10-13 m of water (station 5); and north of Lime Point just inside the Golden Gate Bridge in 25-35 m of water (Station 6). These sites were near those of a previous trawl study (Aplin 1967) and they represented locations from South Bay, Central Bay, the outflow from North Bay, and the Pacific Ocean entrance to the Bay.

All South Bay stations were sampled in one day, all Central Bay stations were sampled on another day, usually the day following the South Bay sampling. This schedule and the pattern of tidal flow in the Bay (Tidal Current Chart, San Francisco Bay 1973) enabled all stations to be sampled before noon at approximately slack tide, low water. This schedule controlled for the effects of time of day, tide, and currents which can affect catches of ichthyoplankton (Eldridge 1977). Additional samples were taken in October 1978 and April 1979 at station 3 and over the shoals adjacent to this station.

Duplicate oblique ichthyoplankton tows and duplicate surface microzooplankton tows were made monthly at six stations for one year, May 1978-April

1979. Ichthyoplankton and zooplankton samples were collected from a 5 m Boston Whaler with a 1 m diameter, cylinder-cone net of 0.308 mm mesh nylon with a 0.200 mm mesh cod end. The net was attached to a sled which kept the lower rim of the net 10 cm above the bottom and which had a tow-bridle that did not obstruct the mouth of the net. A frame attached to the transom permitted the sled to be launched and retrieved over the stern while underway. The sled was lowered to the bottom while underway at 1-2 kn, towed at the bottom for 1 min, and then retrieved at a constant rate and constant wire angle. Tow time, excluding that spent lowering the net to the bottom, was approximately 6 min. The gear was effective because it often caught anchovies and herring longer than 30 mm, a size not usually captured in towed gear (Clarke 1983) or in a plankton purse seine (Murphy and Clutter 1972).

A calibrated flowmeter suspended off-center in the mouth of the net measured the amount of water filtered during the tow. Volumes calculated from the flowmeter readings were similar to a hypothetical volume calculated from net mouth area and tow distance: approximately 300 m^3/tow.

Microzooplankton was collected with a 0.5 m diameter net with 0.080 mm mesh, which was towed just submerged at the surface for 2 min during the ichthyoplankton tow. Because the flowmeter in this net frequently malfunctioned, hypothetical volumes calculated from mouth diameter and tow length (approximately 25 m^3/tow) were used to standardize catches of microzooplankton. The net probably did not filter as much water as calculated so microzooplankton were underestimated. All samples were preserved with 2% formaldehyde in seawater buffered with sodium borate.

Water turbidity was measured with a Secchi disk (Tyler 1968). Water samples for salinity and temperature measurements were taken with a Van Dorn water sampler from 1 m below the surface and from 1 m above the bottom. The temperature was measured to 0.1°C with a laboratory thermometer, and salinity was measured to 0.5‰ with a temperature-compensated refractometer.

Laboratory Procedures

Northern anchovy eggs were easily recognized and distinguished from other regional pelagic fish eggs by their oval shape and their size, approximately 0.75 mm × 1.25 mm. Eggs were not assigned to stages, but some of the embryos were developed enough to be identified as those of northern anchovies. Northern anchovy eggs were counted under a dissecting microscope; at the same time, fish larvae were picked from the samples. The northern anchovy can be separated from other similar looking larvae by its myomere count (43-47), its gut length, and its median fin positions (Miller and Lea 1972; McGowan and Berry 1984).

All northern anchovy larvae <10 mm long were measured to the nearest 0.1 mm using an ocular micrometer. Longer larvae were measured to 1 mm using vernier calipers or a plastic ruler graduated in millimeters. The distance from the tip of the snout to the tip of the notochord was measured in preflexion larvae, standard length in larger specimens.

Zooplankton were subsampled from a 500 mL pharmaceutical beaker by stirring and taking an aliquot with a 1 mL or 2 mL Stempel pipet. Zooplankton were identified to major taxonomic group under the dissecting microscope using standard references such as Smith (1977). All holoplanktonic, meroplanktonic, and nektonic invertebrates were considered to be zooplankton if they were suitably sized prey for adult anchovies. Isopods were included; adult shrimp and gelatinous invertebrates were not. Plankton was allowed to settle in water in a graduated cylinder to estimate zooplankton volume.

Microzooplankton were subsampled from a stirred beaker with a pipet. A settling chamber and inverted compound microscope with movable stage were used to count microzooplankton (0.050-0.200 mm diameter) at 100× magnification. Dinoflagellates known to be eaten by anchovy larvae were counted as microzooplankton.

Precision Estimates

The precision of the microzooplankton counts was estimated by the method of Lund et al. (1958). If the counts are treated as a Poisson variable then the 95% confidence limits for a single count are

$$\text{Upper limit} = X + 2.42 + 1.96(X + 1.5)^{1/2}$$
$$\text{Lower limit} = X + 1.42 - 1.96(X + 0.5)^{1/2}.$$

The limits are approximately ±20% if 100 organisms are counted. Confidence intervals for microzooplankton counts in this study range from ±50% at the lowest count (5) to ±9% at the highest count (659).

The precision of the zooplankton subsampling estimates was evaluated by taking triplicate subsamples, with replacement, from 10 randomly selected samples. The mean coefficient of variation (standard deviation divided by the mean) of the triplicates was 0.29.

The precision of the duplicate tows was evaluated by comparing numbers of eggs, larvae, and zooplankton settled volumes from the May, June, and July tows. No statistical difference was detected between first and second tows (2-tailed $P = 0.407$, Wilcoxon Matched Pairs test, Hull and Nie 1981: 228). The mean coefficient of variation for these paired tows was 0.22. Because there were no statistical differences between these duplicates, only one of each pair of the remaining samples was sorted.

Data Analysis

Eggs, larvae, zooplankton, microzooplankton, and plankton volume per 1,000 m^3 were calculated based on flowmeter readings. Temperature and salinity stratification variables were created by taking the difference between surface and bottom values. Salinity stratification represented the intensity of estuarine circulation or freshwater runoff; temperature stratification represented water column stability and revealed atmospheric temperature extremes.

Distributions of the variables were examined for skewness, kurtosis, and unreasonable range limits indicative of keypunch errors. Normality of the original variables and of $\log(X + 1)$ transformations was tested (Kolmogorov-Smirnov test; Hull and Nie 1981:224). Variances of the transformed variables were not heteroscedastic. Biological and environmental variables were plotted against month, station, and each other to look for spatial patterns, seasonal trends, and nonliner relationships (especially nonmonotonicity) between pairs of variables.

Analysis of variance (ANOVA) was used to assess the effects of month of the year and station location on numbers of eggs and numbers of larvae. Stepwise multiple linear regression was used to examine which of the other variables could account statistically for the variability in numbers of eggs and larvae. Logarithmic transformations of standardized numbers of eggs, larvae, zooplankton, and microzooplankton were used in the regressions and in the ANOVA's.

Ichthyoplankton abundance is often expressed as numbers of ichthyoplankton under an area of sea surface by multiplying density per cubic meter times water depth (Smith and Richardson 1977). In deep water tows are made below the depth range of most eggs and larvae, so the tow depth is used as the effective water depth. Standardizing a unit of sea surface area allows comparisons of total numbers of eggs and larvae in the water column from areas with different water depths. Abundance standardized to area of sea surface was used to estimate total egg production. However, larvae that were relatively uncommon in deep water could be as abundant as more concentrated larvae in shallow water, but exposed to different concentrations of predators and prey; therefore, densities of larvae and plankton were used to examine relationships between ichthyoplankton, other plankton, and environmental variables.

The method used to estimate spawning stock biomass was a direct estimate because it incorporated batch fecundity from histological data (Hunter and Goldberg 1980) and daily egg production estimates from ichthyoplankton surveys (Parker 1980). Parker's equation for the direct estimate of biomass from egg abundance is

$$S = P(ab'c)^{-1}d$$

where S = spawning biomass in tons
P = egg production in eggs/day
a = 3.96×10^8 egg/ton
b' = 0.159 the observed daily spawning fraction
c = 0.550 the proportional biomass of females
d = 1.080 a correction for potential misclassification of daily spawning fraction.

Parker (1980) estimated the coefficient of variation of the estimate of spawning stock to be 0.614. Most of this statistical error was due to error in the estimate of egg production. Daily egg production was estimated in my study by dividing the egg abundance by the number of days needed to hatch at the ambient temperature (interpolated from Zweifel and Lasker 1976, fig. 7).

Numbers per square meter of Bay surface were calculated by multiplying density per cubic meter times water depth at the station. The areas represented by the stations were estimated from the chart of the Bay in Conomos and Peterson (1977). Total numbers of eggs and larvae were calculated from estimates per square meter times the area represented by the sample.

RESULTS

Eggs and Larvae

Either eggs, larvae, or both were present every month of the year. Eggs were present every month except December and January. Only one egg was

collected in February and very few were collected in November. Larvae were present every month and at every station each month with four exceptions: during June, no larvae were collected at station 1, the southernmost station; during July and August no larvae were collected at station 6, the Golden Gate Bridge station; during March no larvae were collected at station 3 in South Bay. Eggs were present on each of the occasions when larvae were absent from the samples.

Egg density varied from 0 to 55,000 per 1,000 m^3 (mean = 3,000). The greatest number of eggs in a single sample was 14,640 at station 2 in July. Occurrence of eggs was seasonal: they were abundant in summer and absent in winter (Fig. 2).

Larvae varied from 0 to 4,400 per 1,000 m^3 (mean = 259). The greatest number of larvae in a single sample was 1,420 in September at station 2. Larval abundance was also seasonal with peak density in late summer and fall (Fig. 2).

Two-way ANOVA of log-transformed standardized densities of eggs and larvae were performed with month and station as fixed factors in separate analyses. The interaction mean square (not significant) was used as the denominator in the *F*-tests because there was just one observation per cell of the design (Montgomery 1976:156). Densities of eggs differed significantly among months ($P < 0.001$, Table 1) but not among stations ($P = 0.104$). Densities of larvae were significantly different among months ($P = 0.010$) and among stations ($P = 0.014$) (Table 2).

Seasonal patterns of abundance of eggs and larvae were unmistakeable, but differences among stations were not as clear so three hypotheses were tested: 1) stations 1, 2, and 3, South Bay stations, differed from stations 4, 5, and 6; 2) stations 4 and 6, Golden Gate and Central Bay stations, differed from stations 1, 2, 3, and 5, South Bay stations plus the station at the outflow of San Pablo Bay; 3) stations 3, 4, and 6, the stations most influenced by ocean water, differed from stations 1, 2, and 5, the Bay stations. These hypotheses were tested using linear contrasts (Nie et al. 1975:425), a procedure that compared the geometric means of the groups of stations.

None of the three contrasts was significant for eggs but all three were significant ($P < 0.05$) for larvae. The difference between the mean of stations 4 and 6 and the mean of stations 1, 2, 3, and 5 was highly significant ($P = 0.001$).

Further comparisons of mean densities of larvae were done using Duncan's Multiple Range test. This a posteriori procedure identified groups of means which did not differ significantly from each other at a specified level (Nie et al. 1975:427). The rank order of the stations in increasing mean density of larvae was 4, 6, 1, 3, 5, 2. Three groupings were produced by the Duncan procedure at the 0.05 level. The mean of stations 4 and 6 was smaller than the mean of the other four. The mean of stations 5 and 2 was greater than that of the other four. Station 4 was significantly lower and station 2 significantly higher than the mean of the other four stations.

A summary of the analyses of variance follows. Eggs and larvae were seasonal in abundance, eggs more strongly than larvae. Numbers of eggs, which would be subject to passive drift and dispersal, were not significantly different among locations in the Bay. Larvae did differ in abundance among the six stations. Based on a priori and a posteriori tests, station 4 and station 6, the stations most influenced by oceanic water, had low densities of larvae while the other stations within the Bay had high mean densities of larvae. This pattern was true for station 5, near the Richmond-San Rafael Bridge, as well as for stations 1, 2, and 3 in the South Bay. Among the within-bay stations, station 1, the southernmost, ranked lowest in both egg density and larval density although it was not statistically different from the other inner stations—2, 3, and 5.

The stations also differed in the proportion of eggs to larvae. While the ratio of eggs to larvae was generally greater than 10:1, at station 3 the ratio of the mean number of eggs to mean number of larvae was <10:1 (Fig. 3). The proportions were statistically different among stations (Chi-square $P <$

TABLE 1.—Analysis of variance of northern anchovy eggs: month by station.

Source of variation	Sum of squares	df	Mean square	*F*	Significance
Residual	42.23	54	0.78		
Constant	286.22	1	286.22	366.02	0.000
Month	128.93	11	11.72	14.99	0.000
Station	7.56	5	1.51	1.93	0.104
Month × station	0.48	1	0.48	0.61	0.437

TABLE 2.—Analysis of variance of northern anchovy larvae: month by station.

Source of variation	Sum of squares	df	Mean square	*F*	Significance
Residual	25.77	54	0.48		
Constant	220.65	1	220.65	462.43	0.000
Month	13.72	11	1.25	2.61	0.010
Station	7.59	5	1.52	3.18	0.014
Month × station	1.16	1	1.16	2.43	0.125

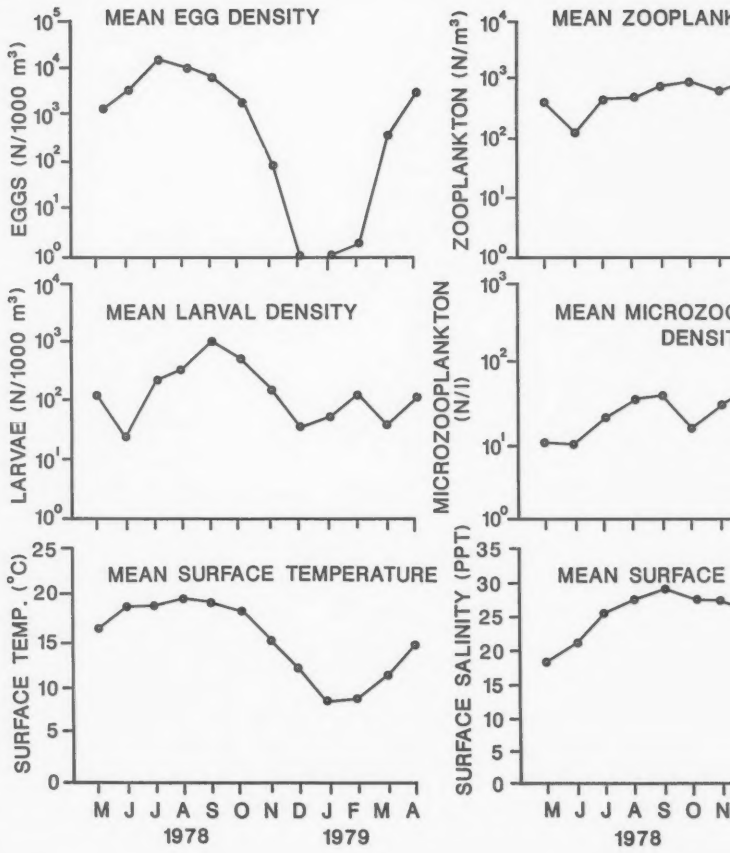
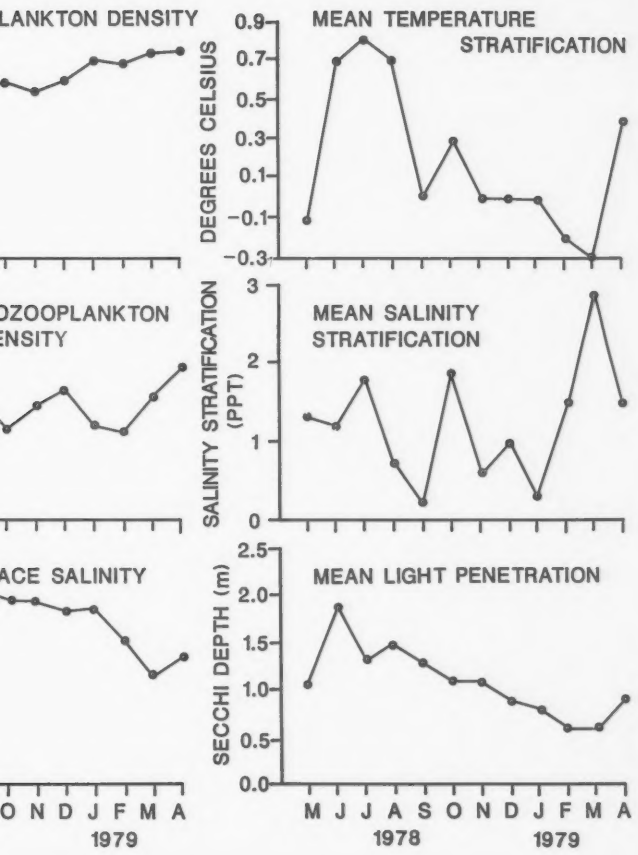


FIGURE 2.—Monthly abundance of northern anchovy eggs, larvae, microzooplankto
surface salinity, temperature stratification, salinity



plankton, zooplankton, and monthly values of surface water temperature,
alinity stratification, and light penetration.

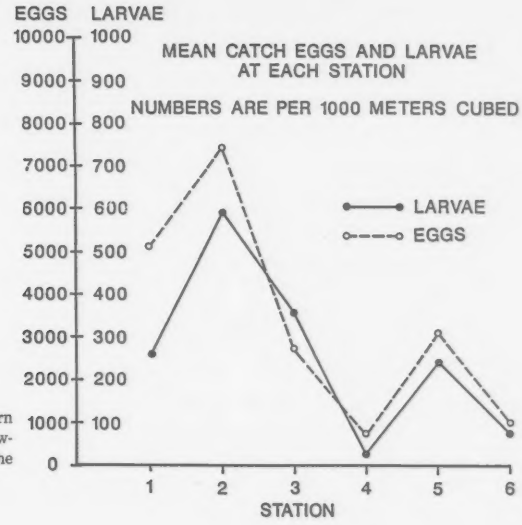


FIGURE 3.—Relative abundances of northern anchovy eggs and larvae at each station showing the difference between station 3 and the other stations.

0.01 with 5 degrees of freedom). Station 3 deviated most from the expected ratio. Station 1 also differed by having relatively fewer larvae than expected.

Zooplankton

Zooplankton catch varied from 13.6-9,560 individuals/m^3. Mean catch was 1,170/m^3. No seasonal pattern was apparent (Fig. 2). There was a gradual increase in zooplankton abundance over the course of the study. This linear trend was significant ($P < 0.01$). Copepods, especially *Acartia* spp., dominated the catches (Table 3). Brachyuran (crab) zooeae and cirrepedian (barnacle) nauplii and cyprids were occasionally abundant. Potential predators on northern anchovy larvae, such as chaetognaths and pontellid copepods, were often present but in relatively low numbers. Counts of zooplankton for each sample are reported in McGowan (unpublished M.A. Thesis, San Francisco State University, San Francisco, CA).

Zooplankton catch was significantly correlated with all variables except surface salinity and salinity stratification. Negative correlations were observed with egg density, surface temperature, temperature stratification, and Secchi depth. Positive correlations were found with larvae and microzooplankton.

TABLE 3.—Zooplankton: relative density, May 1978-April 1979.

Taxon	mean ±1 SE		$n \cdot m^{-3}$	%
Copepoda				
Acartia	1,120	±	192	96.05
harpacticoida	4.67	±	1.55	0.40
other	3.48	±	0.75	0.30
shrimp zoeae	3.82	±	1.28	0.33
crab zoeae	12.27	±	4.27	1.04
mysids	1.31	±	1.16	0.10
amphipods	0.39	±	0.16	0.03
pelecypods	1.10	±	0.35	0.09
chaetognaths	0.59	±	0.23	0.05
polychaetes	1.26	±	0.50	0.11
isopods	0.23	±	0.12	0.02
barnacle nauplii	9.18	±	2.04	0.78
barnacle cyprids	6.18	±	1.49	0.52
gastropods	0.74	±	0.37	0.06
cumaceans	0.08	±	0.05	0.01
cladocerans	0.81	±	0.31	0.07

Microzooplankton

Microzooplankton catch at the surface (0.080 mm mesh net) varied from 1 to 300 per liter (mean = 28.8). No clear seasonal trend was apparent (Fig. 2). Copepod nauplii were the most abundant microzooplankton followed by tintinnids and rotifers (Table 4). Dinoflagellates such as *Ceratium* and *Peridinium* were occasionally more abundant than copepod nauplii. The spiny, armored *Ceratium* species were not included in the density estimates because northern anchovy larvae prefer unarmored forms (Scura and Jerde 1977). Microzooplankton density was negatively correlated with Secchi disk depth ($r = -0.34$, $P = 0.004$) and positively corre-

TABLE 4.—Microzooplankton: relative density, May 1978-April 1979.

Taxon	mean ±1 SE	$n \cdot l^{-1}$	%
copepod nauplii	15.14 ±	1.82	54.97
barnacle nauplii	0.56 ±	0.09	2.03
polychaete larvae	0.36 ±	0.08	1.31
tintinnids	6.56 ±	2.68	23.82
rotifers	1.24 ±	0.45	4.50
harpacticoid copepods	0.03 ±	0.02	0.11
ostracods	0.01 ±	0.01	0.04
gastropod veligers	0.04 ±	0.02	0.15
Peridinium	3.59 ±	1.45	13.03

lated with zooplankton density ($r = 0.27, P = 0.027$). All interpretation of the microzooplankton data was done under the assumption that estimates of volume filtered are accurate.

Environmental Variables

The mean surface water temperature during this study was 15.2°C. The coldest reading was 8.0°C at station 2 in January; the warmest was 22.5°C at station 1 in August (Fig. 2). Water temperature near the bottom varied from 8° to 21.5°C (mean = 15.0°C). Mean temperature stratification, the difference between the surface and bottom temperatures, was 0.2°C. Stratification was generally present June through October, especially at station 5. Mean stratification during these months was 0.5°C (Fig. 2). During February and March 1979 the surface temperature was lower, on average, than the temperature near the bottom thus showing the influence of air temperature on the surface water temperature. Surface salinity varied from 3 to 31‰ (mean = 23.6‰). Bottom salinity was 14-31‰ (mean = 24.8‰). The low readings for both surface and bottom salinity occurred at station 5 during March 1979. Surface salinity at station 1 was usually low, showing the influence of freshwater inflow at the south end of the Bay (Fig. 2). Salinity at station 6 was relatively high, showing the oceanic influence at the Golden Gate. Surface salinity at other stations reflected their relative positions between these two influences. The lowest surface salinity was always at station 5 due to the Sacramento River discharge. During March 1979, salinity at stations 4 and 6 also showed the effects of high freshwater discharge which lowered the salinity at station 5 to 3‰. Salinity was slightly lowered this month at station 3 in South Bay also. Surface salinity followed a seasonal pattern; it was high from July through January and low in the winter and spring months. Relatively high salinity corresponded to high temperature July through October. Salinity stratification was generally <2‰ except at station 5 where the average stratification was 4.7‰ (Fig. 2).

Surface salinity was negatively correlated with salinity stratification, ($r = -0.62, P < 0.001$), and positively correlated with Secchi depth ($r = 0.39$, $P = 0.001$). Salinity stratification was negatively correlated with Secchi depth ($r = -0.29, P = 0.012$).

Turbidity

Light penetration was lowest at stations 1 and 5, and highest at stations 6, 4, and 3 (Fig. 2). The mean depth of light penetration during this study was 1.1 m with a range of 0.1-2.5 m. The data suggest a weak seasonal trend with light transmission higher in summer and lower in winter. The variable with the strongest linear association with Secchi depth was zooplankton density. Light penetration was inversely related to zooplankton density ($r = -0.58$).

Relationships Among Varibles

Northern anchovy egg abundances were positively associated with surface temperature, temperature stratification, and Secchi disk depth and negatively correlated with zooplankton density (Table 5). Eggs were positively associated with larvae but this correlation was not significant at the 5% level ($P = 0.053$). Larvae were positively correlated with surface temperature and zooplankton density (Table 5). They were negatively correlated with Secchi depth. Thus, eggs and larvae both were significantly correlated with zooplankton and Secchi depth but in opposite directions: eggs were associated with clearer water and lower zooplankton density, larvae with more turbid water and higher zooplankton density.

Stepwise Multiple Regression

Surface temperature alone explained 65% of the variability in egg density ($r^2 = 0.651$). The combination of microzooplankton density with surface temperature explains an additional 1.5% of the variability of egg density. The addition of all other variables only increased the amount of variability explained to 68% ($r^2 = 0.678$). The predictive regression model using the independent variables whose addition to the model improved its prediction by more than 1% is

$$E = -2.20 + 0.317T - 0.502M$$

TABLE 5.—Bivariate correlations between northern anchovy eggs, larvae, and other variables. EGGS: log (eggs·m^{-3}); LARV: log (larvae·m^{-3}); ZOOP: log (zooplankters·m^{-3}); MICR: microzooplankton; TEMP: surface water temperature; SALI: surface water salinity; TSTR: temperature stratification; SSTR: salinity stratification; SECC: Secchi disk depth.

	EGGS	LARV	ZOOP	MICR	TEMP	SALI	TSTR	SSTR
LARV	0.23^{+}							
ZOOP	−0.38**	0.29*						
MICR	−0.11	−0.02	0.27*					
TEMP	0.81**	0.31**	−0.46**	0.02				
SALI	0.18	0.08	−0.20	−0.16	0.19			
TSTR	0.40**	0.17	−0.25*	−0.02	0.46**	0.06		
SSTR	−0.10	0.07	0.05	0.09	−0.03	−0.62**	0.12	
SECC	0.35**	−0.34**	−0.58**	−0.34**	0.32**	0.39**	0.20	−0.29*

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
$^{+}$ $P = 0.053$.

where E = log (eggs/1,000 m^3 + 1)
T = surface temperature (°C)
M = log (microzooplankton/l + 1), (Table 6).

No single variable explained the majority of the variability in larval density (Table 7). Secchi depth was the single best predictor, accounting for 11% of the variance of larval density ($r^2 = 0.113$). The combination of surface temperature with Secchi depth increased the coefficient of determination to 0.306. All of the variables combined explained just 50% of the variability of larval density ($r^2 = 0.498$). Five variables improved the prediction of the set of independent variables by more than 1% when added to the model. The predictive equation for larval density based on using these five is

$$L = -0.842 - 0.591X + 0.126T + 0.515Z - 0.571M + 0.029S$$

where L = log (larvae/1,000 m^3 + 1)
X = Secchi depth (m)
T = surface temperature (°C)
Z = log (zooplankton/1,000 m^3 + 1)
M = log (microzooplankton/l + 1)
S = surface salinity (‰).

The results of the multiple regressions show that northern anchovy egg density could be predicted largely by surface water temperature. Larval density could not be predicted well by a single variable or by the five variables which, when combined, accounted for only 49% of the variability.

TABLE 6.—Stepwise multiple regression: northern anchovy egg density vs. biological and environmental variables.

Independent variable	Multiple r^2	Change in r^2
Surface temperature	0.651	0.651
Microzooplankton	0.666	0.015
Salinity stratification	0.670	0.004
Surface salinity	0.672	0.002
Secchi depth	0.675	0.003
Zooplankton	0.677	0.002
Temperature stratification	0.678	0.001

TABLE 7.—Stepwise multiple regression: northern anchovy larval density vs. biological and environmental variables.

Independent variable	Multiple r^2	Change in r^2
Secchi depth	0.113	0.113
Surface temperature	0.306	0.194
Zooplankton	0.392	0.085
Microzooplankton	0.459	0.067
Surface salinity	0.486	0.028
Salinity stratification	0.495	0.009
Temperature stratification	0.498	0.003

Spawning Stock Estimates

Based on estimates of egg production, the spawning stock biomass of northern anchovies in the part of San Francisco Bay sampled in this study ranged from undetectable in December 1978 and January 1979 (no eggs collected) to 696 t (metric tons) (767 short tons) in July 1978. If the area of the Bay which is <2 m deep were included, the estimate of July biomass would have been 2,030 t (2,240 short tons).

Length Frequencies of Larvae

Monthly samples could contain larvae from the current month and 2 previous ones because metamorphosis is not complete until 35 mm, age 74 days at 16°C (Hunter 1976). However, larvae longer than 15 mm were not taken at the standard stations from August through October, although eggs and smaller

larvae had been abundant since June (Fig. 4). Larvae >15 mm long were found over the shoals near station 3 in October and April (Fig. 5). Larvae longer than 15 mm were taken in the channel from November through February, months with little or no spawning. Large larvae and juveniles, which had apparently overwintered, were present when spawning resumed in March and April.

DISCUSSION

Previous suggestions that northern anchovy spawn in San Francisco Bay were based on the presence of small larvae (Eldridge 1977; Sitts and Knight 1979), juveniles (Smith and Kato 1979), or the spawning season in the California Current (Hubbs 1925). Anchovy eggs collected in this study provide conclusive evidence that the northern anchovy spawns in San Francisco Bay because eggs could not drift upstream to station 5 or into South Bay as far as station 1 or 2. Peak spawning based on the abundance of eggs was May through September when adult anchovies are known to be plentiful in the Bay (Aplin 1967).

Spawning in San Francisco Bay differed from anchovy spawning in the sea. Most spawning of the central subpopulation of northern anchovy in the California Current takes place January-April when the 10 m temperature is 14°-16°C; not June through October when water temperature is 16°-19°C

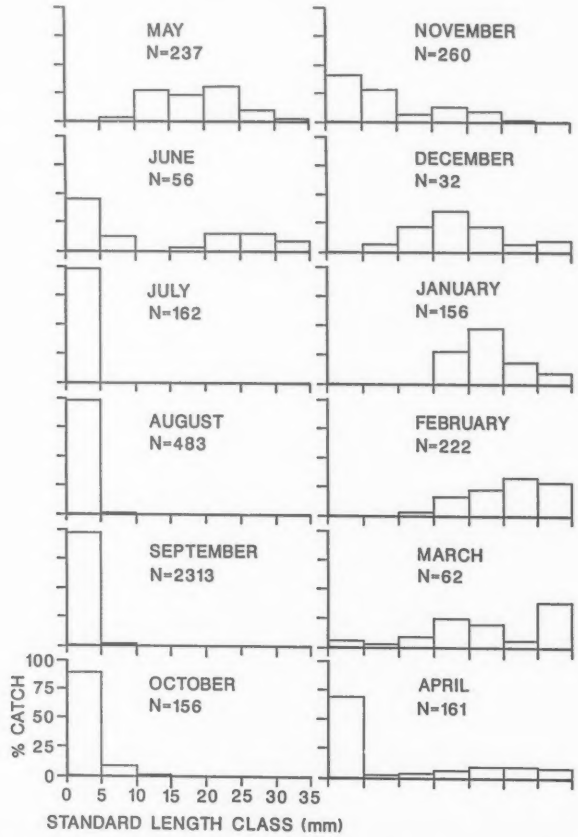


FIGURE 4.—Length-class frequencies of larvae and juvenile northern anchovies for each month of the study.

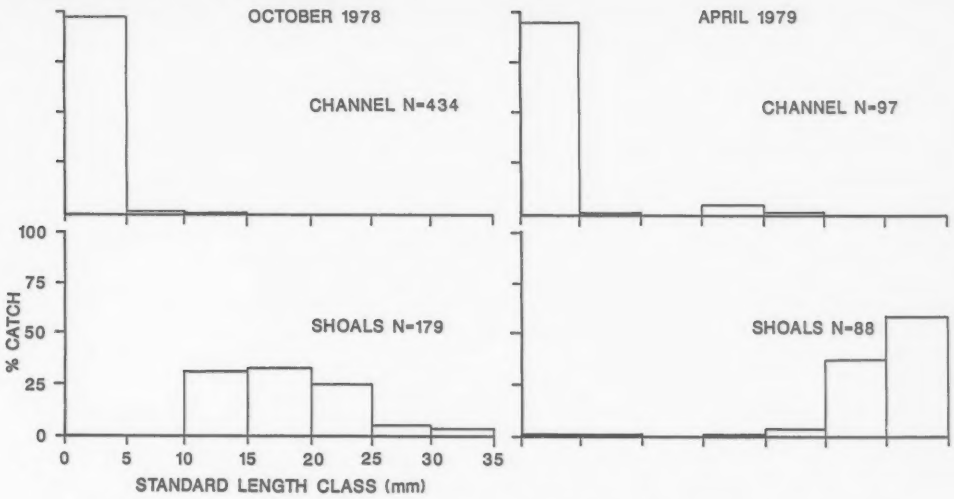


FIGURE 5.—Length-class frequencies of larvae and juvenile northern anchovies for October 1978 and April 1979 showing the different sizes caught in the channel versus those in shallow water.

(Smith and Lasker 1978). The northern subpopulation spawns off Oregon and Washington from mid-June to mid-August when 1 m temperatures are 14°-17°C (Richardson 1980). These two subpopulations overlap at San Francisco (Vrooman et al. 1981) and the spawning season in the Bay overlapped the spawning seasons of both subpopulations. But spawning in the Bay took place at higher temperatures than usual for either population in the ocean (13°-18°C, Brewer 1976). Few eggs were taken in the Bay from December 1978 to March 1979 when water temperature was below 13°C. However, at station 3 in March 1979, 477 eggs were taken at a water temperature of 11.5°C. Peak spawning in the Bay was in July, August, and September when the mean water temperature was 19.0°, 19.8°, and 19.2°C, respectively. The highest catch of eggs occurred at station 2 in July at 21.0°C. Eggs were also plentiful at station 1 in August at 22.5°C. During June, July, and August, eggs were least abundant at stations 4 and 6, where water temperature was relatively low. During September and October, egg densities at stations 4 and 6 peaked, as did water temperature at these stations. Sitts and Knight (1979) found larvae shorter than 4 mm at 18°-22°C in the Sacramento-San Joaquin estuary in July and August. Although much of the northern anchovy spawning took place in the Bay within the previously reported temperature range and some took place at low temperatures, most occurred in water warmer than in the coastal spawning regions. The strong correlation of egg abundance with temperature includes potential confounding effects of presumed seasonal influx of adults, apparent "preference" for spawning within the Bay, and differences in dilution due to tidal exchange which affected stations 4 and 6 more than the other stations. Therefore the correlations are descriptive, perhaps predictive, but not causal.

In the California Current, temperature, upwelling, and stable stratification of the water column are thought to interact to produce favorable conditions for anchovy larvae (Lasker 1975). In San Francisco Bay there is no upwelling, but salinity or freshwater outflow variability might influence ecological conditions. Freshwater flow may have an indirect effect by promoting blooms of certain phytoplankton or by retaining particles through estuarine circulation (Cloern 1979). Relatively high salinity coincided with warm temperatures at the beginning of the spawning season, but spawning ceased in November when water temperature decreased to 13°C, although salinity remained high until February. Sitts and Knight (1979) found larvae shorter than 10 mm at low salinity (<10‰) and relatively high temperature (>18°C). They found only large larvae (>10 mm) in November when water temperature fell below 13°C.

In this study, only temperature had a strong direct relationship with abundance of eggs and larvae;

peak abundance tracked the seasonal temperature cycle closely. Temperature stratification was most pronounced in June-October when spawning was greatest, especially at station 5 where salinity stratification was also most noticeable.

Offshore transport of eggs and larvae is believed to be one of the environmental hazards to anchovy reproductive success (Bakun and Parrish 1982). Peak spawning in the Bay took place in June-August, the months of greatest offshore directed Ekman transport at the latitude of San Francisco (Parrish et al. 1981). Larvae, retained in San Francisco Bay by estuarine circulation or behavior, would not be subject to offshore drift into areas of low plankton density. Therefore, they may have a higher probability of survival than larvae in the California Current and they might survive during bad years for oceanic larvae.

Within San Francisco Bay there were apparent differences between spawning habitat and larval habitat. Eggs and small larvae were more abundant in warm, clear, thermally stratified water with relatively less plankton; large larvae were found in shallow, warm, less stratified, plankton-rich water with reduced light penetration. Negative correlations between zooplankton and the eggs of zooplanktivorous fishes were attributed to predation on the zooplankton by de Ciechomski and Sanchez (1983). Cannibalism on larvae by adult northern anchovies and competition between adults and juveniles are two reasons why separate habitats would be adaptive. Because spawning and nursery habitats differ in location and environmental properties, it is not surprising that multiple regression variables measured in the spawning habitat did not predict larval abundance. It may be that spawning areas are selected by adults, perhaps for feeding (Brewer 1978) or for water clarity, while larger larvae seek different conditions where their survival is determined by other factors than those which affect first-feeding larvae. If variable mortality on the larger larvae determines eventual recruitment, then recruitment may be largely decoupled from spawning and first-feeding conditions. This could explain why predictions of recruitment from larval surveys (which do not adequately sample large larvae and juveniles) have not been reliable.

The conditions where larvae were more abundant are more characteristic of shallow nearshore water than of the California Current. Juveniles and young of the year are also relatively more abundant nearshore in California (Parrish et al. 1986). In 1978, when spawning was restricted to nearshore areas, apparent recruitment was high relative to 1979 when spawning was offshore (Hewitt and Methot 1982). The 1978 spawning season for California Current anchovy was not typical; storms prevented favorable conditions for larvae until March in southern California (Lasker 1981). Nearshore areas might be refugia during anomalous years and they could contribute a disproportionate number of recruits every year (Brewer and Smith 1982).

It might be argued that the 20-30 mm larvae found nearshore in the Southern California Bight (Brewer and Smith 1982) merely avoided the nets in standard CalCOFI tows, but I found a similar pattern with respect to length frequencies when comparing samples taken in the channels and in shallow water in San Francisco Bay. That is, larger larvae were found in shallower zooplankton-rich areas. Estuaries and nearshore areas may provide conditions favorable enough for survival of larvae and juveniles to compensate for low mean food density and for occasional years of unfavorable oceanographic conditions in the California Current.

San Francisco Bay northern anchovy larvae, especially those which overwinter, are subject to different ecological conditions than those in the California Current, thus they may have slightly different morphology and meristics (Hempel and Blaxter 1961; Blaber et al. 1981). The San Francisco Bay subspecies *Engraulis mordax nanus* Hubbs (1925) may be an ecotype of *E. mordax*.

A female northern anchovy has enough energy stored as fat for 17 of its 20 annual batches of eggs, but protein for egg production must come from feeding during the spawning season (Hunter and Dorr 1982). The primary food of northern anchovy, zooplankton, was abundant in the Bay. I found a mean density of 1 zooplankter/L with a 0.308 mm mesh net, but this is an underestimate of copepodites and small copepods because of the relatively large mesh size. By comparison, Hutchinson (1981) found at least order of magnitude greater densities at nearby stations over the same time period using 0.080 and 0.064 mm mesh nets. Anchovy feed by biting individual organisms or by filter-feeding if particle density is high enough. The laboratory-determined threshold for filter-feeding is 5-18 particles (0.236 mm wide) per liter (Hunter and Dorr 1982). My zooplankton density estimate, which was biased conservatively, is of the order of magnitude required to stimulate filter-feeding. Therefore, I conclude that zooplankton prey for adult northern anchovies were abundant in the Bay during this study.

For the Bay to be a good larval nursery area it should have abundant microzooplankton prey for lar-

vae. I found a mean density of 28.8 per liter using a 0.080 mm mesh net (probably a conservative estimate because of net clogging and meter malfunctioning). This is higher than would be expected in the California Current using the same mesh size (<1 per liter, Arthur 1977). It is comparable to the 36 per liter found with a finer mesh net (Arthur 1977). It is an underestimate of available prey for larvae because they consume particles as small as 0.040 mm, and there is a peak of biomass of small plankton in the California Current at 0.070 mm (Arthur 1977), just below the mesh size of my net. Sitts and Knight (1979) found a mean density of 32.3 copepod nauplii/L in a 1-yr study in the Sacramento-San Joaquin estuary using 0.060 mm mesh. Hutchinson (1981) found approximately 10 nauplii/L over the same period of time as this study. (I calculated this value from her data for density of nauplii at 1 m depth at her stations 19 and 30 which correspond to my stations 6 and 2.) My microzooplankton estimates did not adequately represent the rotifers, tintinnids, and other small larval prey which were collected in high numbers with finer mesh nets (Hutchinson 1981). These organisms are known to be eaten by northern anchovy larvae and I observed tintinnids in the guts of some larvae.

Larvae reared in the laboratory generally require more than 1,000 prey items/L for good survival, but some survival occurs at lower densities. Houde (1978) obtained 1% survival to metamorphosis of *Anchoa mitchilli* with a prey density of 27 per liter. Northern anchovy larvae in the sea which obtain enough food to survive also obtain enough to grow rapidly (Methot and Kramer 1979). The existence of dense patches of food has been suggested to account for the discrepancy between average food densities observed in the sea and those needed in the laboratory. Dense patches of larval prey might not be needed in the Bay where I found mean prey density higher than that typical of the California Current. However, dense patches of microzooplankton would be expected in the Bay because blooms of their prey, phytoplankton, occur (Cloern 1982). Dense patches of microzooplankton, undetected by my sampling design, would make San Francisco Bay a very good feeding area for larval northern anchovies. Because the water was warmer in the Bay than in the California Current, larvae could search a larger volume of water per unit time, they would encounter high densities of prey and would be expected to survive in greater numbers and to grow rapidly. Therefore, San Francisco Bay may be a good feeding area for larvae as well as for spawning adults.

To my knowledge, my estimates of spawning biomass of northern anchovies in the Bay are the first such estimates. Are they reasonable, and what are the implications of this biomass of anchovies in the Bay? The estimate based on egg abundance assumes that parameters estimated for California Current anchovies apply to San Francisco Bay anchovies. I argue they do because parameters for the estimate were obtained from anchovies at the peak of spawning in the California Current in 1978, the year my study began. I believe these parameter values may be applied to the anchovy population in San Francisco Bay because the seasonal pattern of spawning and abundance of anchovies in the Bay indicates that most of these anchovies are seasonal migrants from the California Current stocks. No actual measurements of batch fecundity of anchovy in the Bay have been taken so the values used are the best available. Errors in estimating egg and larval abundances are probably more important than small changes in the estimates of batch fecundity. The egg-based estimate could be high if adults leave the Bay immediately after spawning or if they spawn more frequently due to greater food availability. The estimate could be low if they spawn infrequently because the season is later than the regular spawning season in the California Current or if higher temperatures greatly increase metabolic needs.

The estimate is conservatively biased because I merely divided the number of eggs caught by the number of days to hatch at the measured temperature without considering mortality. During the months with peak egg abundance the estimated time to hatch was 2 d. If egg mortality was 0.184 da^{-1} (Picquelle and Hewitt 1984), then the estimate was approximately 25% low. The estimate would be high if eggs were present only in the channel and not over the area used to calculate total abundance. However, station 3, in shallow water near San Bruno Shoal in South San Francisco Bay, had high egg densities; therefore, eggs were distributed in some shallow-water areas. Stations 1 and 2, which had high egg densities, represented small areas, while stations 4 and 6 with low densities represented large areas. San Pablo Bay and the rest of the North Bay were not included in the biomass estimate. Potential biases in the egg-based stock estimate either cancel one another or give a conservative estimate.

My estimate is consistent with information from other studies. I found mean values of 3,360 eggs/1,000 m^3 and 259 larvae/1,000 m^3. Hutchinson (1981) found 4,730 eggs/1,000 m^3 (my calculations from her stations 19 and 30). Sitts and Knight (1979) calculated a mean larval abundance of 490 per 1,000

m^3. The estimates of larval densities are similar to estimates for the Southern California Bight nearshore CalCOFI area in 1978-79 (461 per 1,000 m^3, calculated from table 4 of Brewer and Smith 1982, assuming average tow depth = 210 m; two-thirds of the stations were >210 m according to their table 2). The mean density of eggs in the Bay was much higher than in the Southern California Bight nearshore CalCOFI area (310 per 1,000 m^3, Brewer and Smith 1982). The seasonal northern anchovies fishery in the Bay took approximately 481 tons for frozen and live bait (Smith and Kato 1979). My estimate is adequate to permit such a yield.

Northern anchovy females need a daily ration of 4-5% of their body weight of copepods per day to support growth and reproduction (Hunter and Leong 1981). Approximately 5% of caloric intake goes into growth. Using these values, 38.35 tons of copepods per day would be consumed by the July biomass of 767 tons of anchovies. Growth would be about 1.92 tons per day. Doing similar calculations for each month and summing for the 12 mo of this study result in an estimate of 3,260 tons of copepods consumed and a net annual production of 158 tons of anchovy growth. If the egg estimates based on the area of the Bay, including the shallow areas were used, the consumption of copepods and growth estimates would be approximately doubled. These calculations are a first order estimate of the impact of a carnivorous planktivore on zooplankton in the Bay. The energy converted to anchovy growth would be removed from the Bay, so the estimate of net growth is also a minimum estimate of a sink for Bay production as growth of a transient consumer. In San Francisco Bay where plankton production from a limited area is being consumed by a large, transient anchovy population, grazing by anchovy could conceivably limit zooplankton abundance seasonally. Although it is impossible to distinguish between grazing and interannual differences without estimates of zooplankton production, zooplankton was more abundant in winter 1978-79 when adult anchovies were absent.

A large biomass of planktivores could have other effects on the ecology of the Bay. Selective feeding by clupeoids on larger organisms in lakes can affect the zooplankton community structure (Brooks and Dodson 1965). Northern anchovy schools can also have an impact on nutrient cycling. Smith and Epley (1982) calculated that ambient ammonium concentration would be nearly doubled behind an anchovy school in the Southern California Bight. McCarthy and Whitledge (1972) estimated that nitrogen excretion by the Peruvian anchoveta is an order of magnitude greater than zooplankton excretion, so fish excretion may be the major source of regenerated nitrogen nutrients for phytoplankton production. These high nitrogen inputs would be patchy (Blaxter and Hunter 1982) and their importance would depend on whether or not background levels of nutrients were limiting. Nutrients may not be limiting in San Francisco Bay where light penetration and residence time control phytoplankton dynamics (Cloern 1979). Laboratory studies of copepod productivity, anchovy predation, and nutrient regeneration are needed to define quantitatively the impact of the northern anchovy on plankton dynamics in the Bay. A complete description of the trophic role of anchovy in the Bay should include estimates of zooplankton consumption by larvae, cannibalism by adults, and predation on adult and larval anchovies.

CONCLUSION

San Francisco Bay is a favorable area for northern anchovy spawning because it has abundant food for adults, protection from advective loss for eggs, and abundant food for larvae. There is apparent habitat partitioning between spawning adults and larger larvae which could adaptively reduce predation and competition. Recruitment to the California Current stocks may be determined more by events in the nursery habitat of larvae and juveniles than by conditions favorable for spawning adults and first-feeding larvae; therefore, further work in estuaries and nearshore areas is warranted.

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LITERATURE CITED

APLIN, J. A.
1967. Biological survey of San Francisco Bay, 1963-1966. Calif. Fish Game, Mar. Resour. Oper. Lab. Ref. No. 67-4, 131 p.

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74: 517-530.
1977. Distribution, size, and abundance of microcopepods in the California Current System and their possible influence on survival of marine teleost larvae. Fish. Bull., U.S. 75: 601-611.

BAKUN, A., AND R. H. PARRISH.
1982. Turbulence, transport, and pelagic fish in the California and Peru current systems. CalCOFI Rep. 23:99-112.

BLABER, S. J., D. P. CYRUS, AND A. K. WHITFIELD.
1981. The influence of zooplankton food resources on the morphology of the estuarine clupeid *Gilchristella aestuarius* (Gilchrist, 1914). Environ. Biol. Fish. 6:351-355.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 1-223.

BREWER, G. D.
1976. Thermal tolerance and resistance of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:433-445.
1978. Reproduction and spawning of the northern anchovy, *Engraulis mordax*, in San Pedro Bay, California. Calif. Fish Game 64:175-184.

BREWER, G. D., AND P. E. SMITH.
1982. Northern anchovy and Pacific sardine spawning off Southern California during 1978-1980: preliminary observations on the importance of the nearshore coastal region. CalCOFI Rep. 23:160-171.

BROOKS, J. L., AND S. I. DODSON.
1965. Predation, body size, and composition of plankton. Science 150:28-35.

CLARKE, T. A.
1983. Comparison of abundance estimates of small fishes by three towed nets and preliminary results of the use of small purse seines as sampling devices. Biol. Oceanogr. 2:311-340.

CLOERN, J. E.
1979. Phytoplankton ecology of the San Francisco Bay system: the status of our current understanding. *In* T. J. Conomos (editor), San Francisco Bay: the urbanized estuary, p. 247-264. AAAS Pac. Div., San Franc., CA.
1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? Mar. Ecol. Prog. Ser. 9:191-202.

CONOMOS, T. J., AND D. H. PETERSON.
1977. Suspended particle transport and circulation in San Francisco Bay: an overview. *In* M. Wiley (editor), Estuarine processes, Vol. 2, p. 82-97. Acad. Press, N.Y.

DE CIECHOMSKI, J. D., AND R. P. SANCHEZ.
1983. Relationship between ichthyoplankton abundance and associated zooplankton biomass in the shelf waters off Argentina. Biol. Oceanogr. 3:77-101.

ELDRIDGE, M. B.
1977. Factors influencing distribution of fish eggs and larvae over eight 24-hr samplings in Richardson Bay, California. Calif. Fish Game 63:100-116.

HEMPEL, G., AND J. H. S. BLAXTER.
1961. The experimental modification of meristic characters in herring (*Clupea harengus* L.). J. Cons. Perm. Explor. Mer 26:336-346.

HEWITT, R. P., AND R. D. METHOT JR.
1982. Distribution and mortality of northern anchovy larvae in 1978 and 1979. CalCOFI Rep. 23:226-245.

HOUDE, E. D.
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395-411.

HUBBS, C. L.
1925. Racial and seasonal variation in the Pacific herring, California sardine, and California anchovy. Calif. Fish Game, Fish Bull. 8, 23 p.

HULL, C. H., AND N. H. NIE (editors).
1981. SPSS update 7-9. McGraw-Hill Book Co., N.Y.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

HUNTER, J. R., AND H. DORR.
1982. Thresholds for filter feeding in northern anchovy, *Engraulis mordax*. CalCOFI Rep. 23:198-204.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

HUTCHINSON, A.
1981. Zooplankton species composition and abundance in the South Bay, 1978-1979. U.S. Geol. Surv. Open File Rep. 81-132.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177:322-354.
1981. Marine fish larvae. Univ. Wash. Press, Seattle, 131 p.

LUND, J. W. G., C. KIPLING, AND E. D. LECREN.
1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11:143-170.

MCCARTHY, J. J., AND T. E. WHITLEDGE.
1972. Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*). Fish. Bull., U.S. 70:395-401.

MCGOWAN, M. F., AND F. H. BERRY.
1984. Clupeiformes: development and relationships. *In* H. G. Moser et al. (editors), Ontogeny and systematics of fishes, p. 108-126. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1, 760 p.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engralis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Fish Game, Fish Bull. 157, 235 p.

MONTGOMERY, D. C.
1976. Design and analysis of experiments. John Wiley & Sons, N.Y., 418 p.

MURPHY, G. I., AND R. I. CLUTTER.
1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. SPSS: statistical package for the social sciences. 2d ed. McGraw-Hill Book Co., N.Y.

PARKER, K.
1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78:541-544.

PARRISH, R. H., D. L. MALLICOATE, AND K. F. MAIS.
1986. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:483-496.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

PICQUELLE, S. J., AND R. P. HEWITT.
1984. The 1983 spawning biomass of the northern anchovy. CalCOFI Rep. 25:16-27.

RECKSIEK, C. W., AND H. W. FREY.
1978. Biological, oceanographic, and acoustical aspects of the market squid, *Loligo opalescens* Berry. Calif. Fish Game, Fish Bull. 169:1-185.

RICHARDSON, S. L.
1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855-876.

SCURA, E. D., AND C. W. JERDE.
1977. Various species of phytoplankton as food for larval northern anchovy *Engraulis mordax*, and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fish. Bull., U.S. 75:577-583.

SITTS, R. M., AND A. W. KNIGHT.
1979. Plankton ecology in the Sacramento-San Joaquin estuary. Water Sci. Eng. Pap. No. 4509, 145 p. Univ. Calif. Davis, Davis, CA.

SMITH, D. L.
1977. A guide to marine coastal plankton and marine invertebrate larvae. Kendall/Hunt Publ. Co., Dubuque, IA.

SMITH, P. E., AND R. W. EPPLEY.
1982. Primary production and the anchovy population in the Southern California Bight. Limnol. Oceanogr. 27:1-17.

SMITH, P. E., AND R. LASKER.
1978. Position of larval fish in an ecosystem. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:77-84.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. No. 175, Rome.

SMITH, S. W., AND S. KATO.
1979. The fisheries of San Francisco Bay: past, present, and future. *In* J. T. Conomos (editor), San Francisco Bay: the urbanized estuary, p. 445-468. AAAS Pac. Div., San Franc., CA.

TYLER, J. E.
1968. The Secchi disk. Limnol. Oceanogr. 13:1-6.

VROOMAN, A. M., P. A. PALOMA, AND J. R. ZWEIFEL.
1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*. Calif. Fish Game 67:39-51.

WANG, J. C.
1981. Taxonomy of the early life stages of fishes: fishes of the Sacramento-San Joaquin estuary and Moss Landing Harbor-Elkhorn Slough, California. Ecological Analysts, Inc., Concord, CA., 168 p.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes - a general model. Fish. Bull., U.S. 74:609-621.

THE SPAWNING FREQUENCY OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, FROM THE SOUTH PACIFIC

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ABSTRACT

Histological criteria to age postovulatory follicles were developed from examination of laboratory-spawned skipjack tuna; the criteria were used to estimate the frequency of spawning of skipjack tuna from the South Pacific. Examination of 87 skipjack tuna from field collections taken in October-November indicated that spawning occurred nearly every day. The fraction of mature females with postovulatory follicles, <24 hours old, was 0.85 (standard deviation = 0.071) indicating that the mean interval between spawnings was only 1.18 days.

Estimates of the frequency of spawning of multiple spawning fishes are essential for understanding their reproductive biology. To estimate annual reproductive effort or fecundity, and how these variables are related to size or age structure of a population requires knowledge of the frequency of spawning and the number of eggs produced per spawning. Batch fecundity, the number of eggs produced per spawning, has been estimated for skipjack tuna a number of times (see review by Matsumoto et al. 1984) but the spawning rate of the skipjack is unknown. Thus spawning frequency is one of the missing links in an assessment of the reproduction of skipjack populations.

It has long been recognized that skipjack tuna spawn more than once in a season because more than one mode of advanced oocytes are found in active ovaries (Brock 1954; Buñag 1956; Joseph 1963; Raju 1964; Simmons 1969; Batts 1972; Cayré 1981; Goldberg and Au 1986). The frequency of occurrence of female black skipjack tuna, *Euthynnus lineatus*, throughout the spawning season with ovaries containing hydrated oocytes led Schaefer (1986) to conclude that the average interval between spawnings of black skipjack in the eastern tropical Pacific was 2.1-5.7 d depending on the region.

Over the last 6 years, two methods have been developed for measuring the spawning rate of multiple spawning marine fishes: One method is based on the frequency of ovaries containing hydrated oocytes and the other is based on the frequency with which they contain postovulatory follicles of known age (Hunter and Macewicz 1985a). These methods have been used to measure the rate of spawning in a number of marine fishes: *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980); *Engraulis ringens* (Alheit et al. 1984); *Hypsoblennius jenkinsi* (Present 1985); *Sardinella brasiliensis* (Isaac-Nahum et al. 1985); *Seriphus politus* (DeMartini and Fountain 1981); and *Euthynnus lineatus* (Schaefer 1986). Postovulatory follicles were used in most studies, but DeMartini and Fountain (1981) and Schaefer (1986) used the incidence of females with hydrated oocytes to estimate spawning frequency. The hydrated oocyte method may produce a biased estimate in some species because of increased vulnerability of hydrated females to netting gear (Alheit et al. 1984).

The objective of this paper was to estimate the spawning rate of South Pacific skipjack tuna by applying some of these techniques. It was not possible to use the hydrated ovary method in our study because fish were not caught during the period of the day when the ovary was hydrated. Instead, we used the incidence of females having ovaries containing postovulatory follicles to estimate the frequency of spawning of skipjack tuna. This method requires ovaries to be preserved immediately in formaldehyde solution when the fish is caught, a histological examination of the ovary, and the development of a staging system for estimating the age of the postovulatory follicle. Our histological classification included not only an assessment of spawning frequency but also an assessment of the extent of ovarian atresia. The atretic condition of the ovary is a sensitive index of the reproductive state of

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females during the spawning season and can be used to identify females approaching the end of their spawning season as well as those in postspawning condition (Hunter and Macewicz 1985b).

METHODS

Skipjack tuna were captured either by pole and line or were catches associated with moored fish attraction devices or free floating natural flotsam. Two sets of collections of skipjack tuna were analyzed: a group of 12 females taken near Noumea, New Caledonia on 23 February 1984; and a group of 87 females taken in 8 different collections at various locations in the South Pacific from 20 October to 30 November 1984 (Table 1). Our samples were opportunistically taken and spanned a great latitudinal range (0°-23°S). At present the peak spawning months of skipjack tuna are poorly defined over this range of latitudes. Spawning is known to occur throughout the year in some areas (Nishikawa et al. 1985), but regional differences may exist in the peak months of spawning, and the spawning season also varies with skipjack size (Naganuma 1979). Naganuma concluded from analysis of gonosomatic indices (GSI) that peak spawning period for small skipjack tuna (40-60 cm) in the South Pacific is October to December. Argue et al. (1983) examined 11,000 adult skipjack tuna for cannibalism of juveniles (15-70 mm) and for GSI over the same latitude range as this study, but covering 80° of longitude (140°W-140°E). They found that cannibalism and female GSI was highest between October and March in this broad area. More data are needed to identify the regional variation about this general pattern.

The 8 collections of gonads (collections 2-9, Table 1) were treated statistically as 8 "clusters" of random samples of unequal size. The mean proportion of postovulatory follicles <24 h old was calculated as the total number of females with such follicles divided by the total number of mature females. Cochran (1977) pointed out that estimation of variance by the simple binomial probability formula can produce serious errors. The variance was calculated by the appropriate formula recommended by Cochran (1977).

TABLE 1.—Characteristics of 9 collections of female skipjack tuna taken in the South Pacific in 1984.

Collection number	Date	Time of day (h)	N	Fork length Mean (cm)	Fork length Range (cm)	Gear[1]	Lat.[2] S	Long.[2] E
1	2-23-84	0800	12	47	44-51	PL	23.00	167.00
2	10-20-84	0745	7	49	46-50	PS	16.	178-179
3	10-23-84	0700	6	48	46-52	PS	16.	178-179
4	10-24-84	0700	8	49	46-52	PS	16.	178-179
5	10-25-84	0700	7	50	47-52	PS	16.	178-179
6	10-26-84	0700	14	49	45-51	PS	16.	178-179
7	10-27-84	0645	8	48	46-50	PS	16.	178-179
8	11-19-84	0755	25	50	44-62	PS	03.41	144.08
9	11-30-84	1955	12	56	49-60	PS	0.03	147.46

[1]PL = pole and line; PS = purse seine catch of skipjack tuna attracted to either a fish attraction device moored in waters of 350-450 m deep or natural flotsam.
[2]Latitude and longitude given in degrees and minutes when available.

Three female skipjack tuna were spawned in captivity (23°-24°C; June 1985) at the Kewalo Research Facility of the National Marine Fisheries Service using the stress spawning technique of Kaya et al. (1982). One fish (48 cm fork length [FL]) was sacrificed at the time of spawning, another (43.8 cm FL) 12 h later and the third (44 cm FL) 24 h after spawning. The ovaries of these females were used to establish histological criteria for the aging of the postovulatory follicles of the sea-caught females.

Ovaries were preserved in 10% Formalin[3] and embedded in Paraplast. Histological sections were cut at 5-6 μm and stained with Harris hematoxylin followed by eosin-phloxine-B counter stain (H&E).

Histological Classification

To estimate reproductive condition of skipjack tuna, we used two histological classification systems: one for estimating spawning frequency and the other for assessing the likelihood that a female will continue to spawn (atretic state of the ovary). Each ovary was classified histologically according to both systems. These classification systems were developed for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980) and Hunter and Macewicz (1980, 1985a, b) and are used here with a few modifications appropriate to skipjack tuna ovarian structure and their rates of postovulatory follicle resorption. The descriptions of postovulatory follicles of different ages are from the three captive Hawaiian skipjack tuna. As these fish resorbed their postovulatory follicles much more rapidly than did the northern anchovy, we used stages of shorter duration. The atretic classification system remains unchanged, except for a few minor details of histological structure based on our observations of sea-caught fish. We believe that the reproductive interpretations we associate with the atretic classes are

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

meaningful because the oocyte resorption seems to follow a similar sequence of stages in most teleosts (Bretschneider and Duyvene de Wit 1947; Lambert 1970). The rate a skipjack tuna ovary passes from one atretic state to another is not specified and would require an additional study of captive fish. The characteristics of the two classification systems are outlined below.

Spawning Frequency

Hydrated and Migratory Nucleus Stages

Ovaries with many translucent hydrated oocytes (oocytes enlarged by fluid uptake just prior to ovulation) are classified in the hydrated stage. Spawning is considered to be imminent. In northern anchovy, spawning takes place in <12 h after the onset of hydration. No skipjack tuna with hydrated oocytes were taken in our field collections. Female skipjack tuna were taken with ovaries in the migratory nucleus stage. This stage occurs just before the onset of hydration and is characterized by the migration of the nucleus to the animal pole of the oocyte and the beginning of the fusion of its yolk globules (Fig. 1).

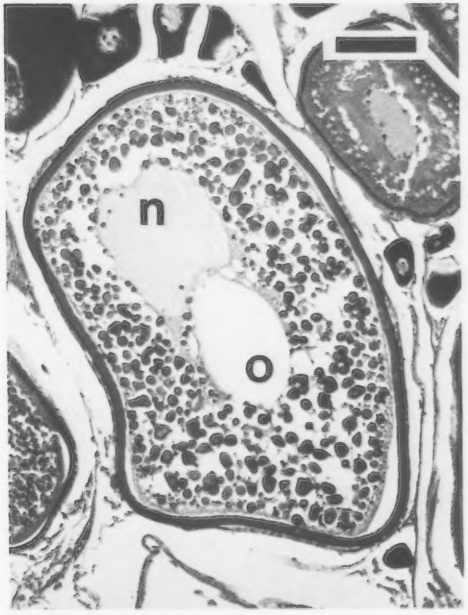

FIGURE 1.—Skipjack tuna oocyte with migratory nucleus (n) and large oil droplet (o); bar = 0.1 mm.

Age 0-H Postovulatory Follicles

Ovaries with new postovulatory follicles with no signs of follicle degeneration are classed as age 0-h postovulatory follicles. Hydrated oocytes may occasionally be present. Estimated elapsed time from spawning is 0-2 h. No skipjack tuna taken at sea were in this stage, but from the laboratory specimen (Fig. 2a, b) we can discern the following histological characteristics: The new postovulatory follicle has an irregular, convoluted shape. The granulosa epithelial cell layer of the follicle appears as an irregularly looped cord of slightly hypertrophied cuboidal cells with prominent healthy nuclei linearly arranged. The granulosa appears only loosely attached to the thecal connective tissue layer. Although the theca is less convoluted than the granulosa layer, it is distinct, contains blood capillaries and appears thicker than the thecal layer seen in northern anchovy.

Age 12-H Postovulatory Follicles

Twelve-hour-old postovulatory follicles (Fig. 2c, d) show signs of degeneration similar to that observed in northern anchovy after about 24 h. Histological characteristics include the follicle which is smaller with fewer convolutions; a lumen which is evident; the degenerating granulosa which is no longer a recognizable unbroken cord of cells, but rather the cells are scattered in clumps in the lumen or may be irregularly attached to the theca; and some pycnotic or irregular nuclei which are evident. The theca has begun to disintegrate although it still remains thick and distinct. Deterioration of the theca is indicated by its overall smaller size, a more filamentous rather than cohesize cellular arrangement, and some irregular nuclei.

Age 24-H Postovulatory Follicles

Ovaries containing 24-h-old postovulatory follicles showed pronounced signs of degeneration similar to that observed in northern anchovy 48 h after spawning. At this stage the follicle is much smaller than that at 12 h but a lumen is still evident (Fig. 2e, f). Only few granulosa cells remain; they usually have pycnotic nuclei and generally are loosely attached to the thecal layer. The thecal layer is still fairly thick although it contains some pycnotic

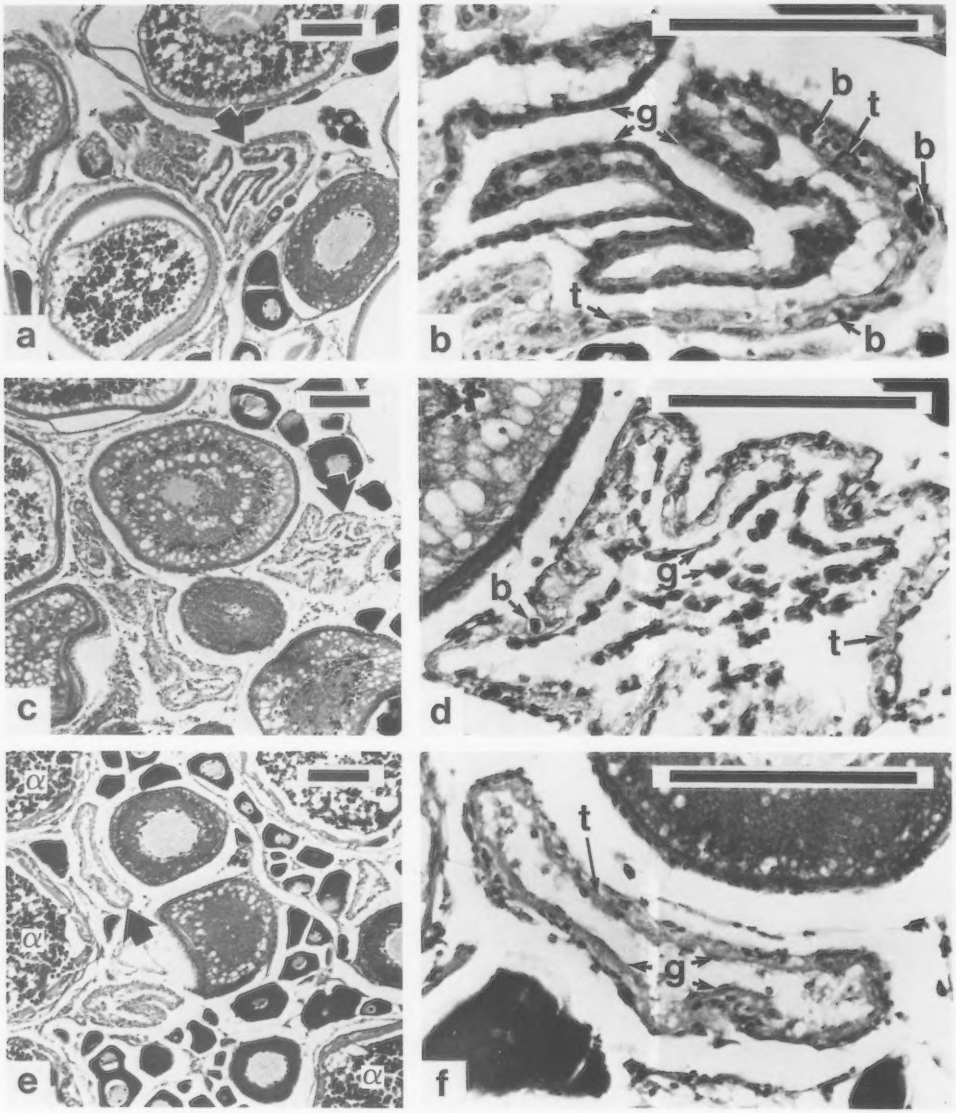

FIGURE 2.—Degeneration of postovulatory follicles of skipjack tuna spawned in the laboratory. Arrow in left panel indicates the postovulatory follicle that is seen under a higher magnification in right panel. a and b, 0 h after spawning (no deterioration); c and d, 12 h after spawning (pronounced degeneration); and e and f, 24 h after spawning (little remains of the degenerating postovulatory follicle). Bar = 0.1 mm; g = granulosa epithelial cell layer; t = thecal cell layer; b = red blood cell(s); and α = early alpha stage atretic oocytes.

nuclei, and lymphocytes, and has a more filamentous composition.

Nonspawning (mature)

Ovaries with many yolked oocytes and containing no hydrated oocytes or postovulatory follicles were classified as nonspawning. They may contain postovulatory follicles in advanced stages of degeneration which cannot be readily distinguished from late stage corpora atretica. Elapsed time from spawning was more than 24 h. Also classified as nonspawning (mature) were females in postspawning condition. The ovaries of such females contained no yolked oocytes, but atretic follicles (beta stage) were present indicating that the ovary was active recently (see next section).

Immature

Ovaries containing no yolked oocytes and no α or β stage atretic structures were classed as immature.

Atretic States

It is well known in seasonal spawning fishes that a low incidence of atresia (resorption of the oocyte and its follicle) occurs throughout the spawning season, but it becomes marked as the spawning season closes and the remaining advanced oocytes in the ovary are resorbed. During the initial atretic phase (α), the oocyte is resorbed and any yolk globules are broken down and resorbed by the hypertrophying granulosa cells of the follicle (Bretschneider and Duyvene de Wit 1947; Lambert 1970). In the next stage (β), all the yolk is gone, and there remains a small, rather compact structure with one or more cavities. The structure is composed of granulosa and theca cells with penetrating blood vessels. Further stages of follicle resorption have been described by the same authors, but the incidence and extent of α and β stages have proven to be the most useful in the classification of atretic states of ovaries (Hunter and Macewicz 1985b). The characteristics of α and β atretic structures are described and illustrated for northern anchovy by Hunter and Macewicz (1985b) and α atretic oocytes of skipjack tuna are essentially similar. However, β atresia differs from northern anchovy in containing numerous spherical vacuoles scattered throughout the follicle. The vacuoles are the remnants of the oil droplet which takes longer than yolk to resorb and in H&E sections appear empty. Occasionally, a large beta stage follicle may be seen in which the granulosa and thecal cells have proliferated.

Listed below are the characteristics of the four atretic states we used to classify skipjack tuna ovaries along with what is known regarding the spawning potential of northern anchovy classed in these states.

Atretic State 0

Yolked oocytes present, with no α atresia of yolked oocytes; β stage atresia may be present, but it cannot be distinguished with certainty from late stage postovulatory follicles (>24 h old). Female northern anchovy in this state have a high potential of spawning.

Atretic State 1

Less than 50% of the yolked oocytes are in the α stage of atresia. The frequency of spawning for northern anchovy classed in this state is less than half of that for females classed in atretic state 0. Thus, atretic state 1 indicates a decline in spawning rate.

Atretic State 2

Fifty percent or more of the yolked oocytes are in the α stage of atresia. The frequency of spawning for female northern anchovy classed in this state is very low and indicates that cessation of spawning is imminent.

Atretic State 3

Ovaries contain β stage atresia and no yolked oocytes. Such fish have completed their spawning season since they have no yolked oocytes. The presence of β stage atresia indicates that oocyte resorption has taken place and thereby distinguishes such recently mature but postspawning fish from immature females. In northern anchovy, atretic state 3 may persist for 30 d.

RESULTS AND DISCUSSION

All postovulatory follicles in sea-caught skipjack were less degenerated than those observed in a laboratory specimen examined 24 h after spawning, indicating that all of those in the sea collections were <24 h old. The fraction of mature females with postovulatory follicles <24 h old ([55 + 18]/86, Table 2) was 0.85 with the standard deviation estimated to

TABLE 2.—Numbers of female skipjack tuna in various spawning and atretic states. The 8 collections taken in the South Pacific between 20 October and 30 November 1984.

Collection number	Atretic state[1]	Age (A) Postovulatory follicles (h) A ⩽ 12	12 < A < 24	Non-spawning	Total mature females
2	0	0	0	2	2
	1	1	0	2	3
	2	0	0	1	1
	3	0	0	1	1
	Total	1	0	6	7
3	0	1	0	1	2
	1	4	0	0	4
	2	0	0	0	0
	3	0	0	0	0
	Total	5	0	1	6
[2]4	0	3	0	0	3
	1	3	0	0	3
	2	1	0	0	1
	3	0	0	0	0
	Total	7	0	0	7
5	0	3	0	0	3
	1	2	0	0	2
	2	1	1	0	2
	3	0	0	0	0
	Total	6	1	0	7
6	0	9	0	0	9
	1	5	0	0	5
	2	0	0	0	0
	3	0	0	0	0
	Total	14	0	0	14
7	0	3	0	0	3
	1	5	0	0	5
	2	0	0	0	0
	3	0	0	0	0
	Total	8	0	0	8
8	0	8	5	0	13
	1	5	2	1	8
	2	[3]1	0	2	3
	3	0	0	1	1
	Total	14	7	4	25
9	0	0	[4]4	[5]2	6
	1	0	[6]6	0	6
	2	0	0	0	0
	3	0	0	0	0
	Total	0	10	2	12
2-9	0	27	9	5	41
	1	25	8	3	36
	2	3	1	3	7
	3	0	0	2	2
	Total	55	18	13	86

[1]Atretic State 0 = no alpha stage atresia of yolked oocytes.
State 1 = alpha stage atresia of yolked oocytes present, but <50% affected.
State 2 = alpha stage atresia present, 50% or more yolked oocytes affected.
State 3 = no yolked oocytes present and beta stage atresia present.
[2]One female skipjack tuna in collection 4 was immature.
[3]A female with hydrated oocytes and age 0 h postovulatory follicles.
[4]Three of these females had oocytes in migratory nucleus stage.
[5]Two of these females had oocytes in migratory nucleus stage.
[6]Five of these females had oocytes in migratory nucleus stage.

be 0.071 (Cochran 1977; see methods). This means that the average interval between spawnings (1/0.85) was only 1.18 d. Only one female was immature, reducing the denominator for the above fraction spawning from 87 to 86. If we consider only those females with yolked oocytes and no or minor atresia (atretic states 0 and 1) the fraction spawning is 0.90, implying a mean interval of 1.11 d between spawnings. This indicates that the spawning rate of female skipjack tuna in prime reproductive condition is very close to daily.

High levels of ovarian atresia were much more common among the 12 females taken in February than those taken in October-November, indicating that the February fish were nearing the end of their spawning season. Females with highly atretic ovaries (state 2) and postspawning ovaries (state 3) constituted 66% of the fish in the February collections (Table 3), but they made up only 10% of the fish taken in October-November. The February collection was the only one taken by pole and line. It is possible that pole-and-line fishing may be selective against spawning fish (Iverson et al. 1970; Matsumoto et al. 1984) although some spawning fish were taken in this collection.

The most unusual feature of the February collection was that the spawning fraction was high, 0.25 for a group where 50% of the fish were in postspawning condition, had no yolked oocytes, and were incapable of spawning (atretic state 3). The spawning fraction was 1.0 for the three females with no or minor atresia because all three had postovulatory follicles. Thus skipjack tuna with active ovaries appear to spawn nearly every day. It appears that those unable to maintain this rate may discontinue spawning and resorb the ovary because females with active ovaries, showing no evidence of spawning, were rare in all collections. Postspawning females

TABLE 3.—Numbers of female skipjack tuna in various spawning and atretic states. This single collection was taken 23 February 1984.

Collection number	Atretic state[1]	Postovulatory follicles 12 h	24 h	Non-spawning	Total mature females
1	0	2	0	0	2
	1	1	0	1	2
	2	0	0	2	2
	3	0	0	6	6
	Total	3	0	9	12

[1]Atretic State 0 = no alpha stage atresia of yolked oocytes.
State 1 = alpha stage atresia of yolked oocytes present, but <50% affected.
State 2 = alpha stage atresia present, 50% or more yolked oocytes affected.
State 3 = no yolked oocytes present and beta stage atresia present.

might reactivate their ovary sometime later in the year if their physiological condition favored reproduction. Evidence for northern anchovy indicates that the transitions from spawning to postspawning states and vice versa can occur rapidly. In the laboratory at 16°C, northern anchovy can resorb all advanced oocytes within a few weeks (Hunter and Macewicz 1985b) and can produce an active ovary in 30 d (Hunter and Leong 1981). Owing to the higher water temperatures and high metabolism of skipjack tuna they are probably capable of even faster reproductive cycling.

Histological examination of females taken late in the day (1955 h, collection 9) provided additional evidence for daily spawning. Eight of 10 females with postovulatory follicles in this collection also had oocytes in the migratory nucleus stage. This stage is the precursor to hydration. Thus, fish which had spawned <24 h before were beginning to hydrate a new batch of eggs which presumably would be spawned in <12 h. The migratory nucleus stage was observed only in this collection probably because it was the only one taken in the evening, whereas all others were taken in the morning (0645-0755). The rarity of females with hydrated oocytes in our collections and the age of the postovulatory follicles imply that spawning usually took place at night. Spawning in daylight hours has been observed by fishermen and scientists, however (Iverson et al. 1970; Matsumoto et al. 1984).

A single female taken during the morning (collection 8) had small (0.70 mm) early stage hydrated oocytes (hydrated oocytes in which the yolk globules had not fully fused). This female, the only one with hydrated oocytes in our collections, also had new postovulatory follicles despite the fact that the hydrated oocytes were not fully advanced. This female may have been induced to hydrate and spawn by the stress of capture or may be simply an exception to the rule. To capture significant numbers of females with hydrated oocytes would probably require sampling after 2100 h. It is important to capture eventually some females in the hydrated stage because it is the best way to confirm that all oocytes in the most advanced modal group, the group of oocytes considered to be the next spawning batch (Hunter and Goldberg 1980), are in fact spawned. Counts of hydrated eggs are also the easiest and most accurate method of estimating batch fecundity (Hunter et al. 1985).

The "stress" spawning technique of Kaya et al. (1982) was used to produce the spawned skipjack tuna for the aging of postovulatory follicles. In this technique females captured at sea and placed in a tank spawn spontaneously, usually about 8 h after capture presumably because of the stress of capture and handling. Spawning typically takes place at about 2400 h, which, by our estimate, appears to be close to the usual time of spawning. It now seems likely that many of these fish are naturally expressing their daily spawning activity. On the other hand, eggs less than the normal size range, 0.8-1.17 mm (Matsumoto et al. 1984), are occasionally spawned, indicating that stress may induce premature hydration in some individuals. That the skipjack tuna do not continue to spawn in the tanks is due probably to the stress of captivity. Our examination of a captive skipjack 24 h after spawning indicated that nearly all remaining oocytes containing yolk were in the early stages of alpha atresia (Fig. 2e). Similarly, female northern anchovy nearly always resorb their advanced oocytes a few days after capture although they will subsequently mature and spawn (Leong 1971; Hunter and Macewicz 1985b).

If female skipjack tuna spawn at the frequency we observed (85% of the females per day), the cost of reproduction and annual fecundity will be high because skipjack tuna appear to have a long spawning season. The relative batch fecundity of skipjack (number of eggs per spawning per body weight) is about 100 eggs per gram (Matsumoto et al. 1984; Goldberg and Au 1985). Skipjack tuna eggs are about the same size as those of *Scomber japonicus* which average in weight 0.04 mg (unpubl. data, National Marine Fisheries Service, Southwest Fisheries Center). We estimate the cost of a single spawning (excluding the metabolic cost of egg maturation and reproductive behavior) to be about 2% of the body weight per spawning (*Scomber* egg dry weight × relative batch fecundity × conversion to wet weight; $4 \times 10^{-5} \times 100 \times 5 = 0.02$). If a female spawned every 1.18 d over 3 mo (90 d), it would produce about 7,600 eggs per gram body weight at an average daily cost of 1.7% of the body weight per day; a 4 kg skipjack tuna would spawn about 30 million eggs over this period.

If the collections used in this study were an unbiased sample of the South Pacific skipjack tuna population, then little doubt exists that spawning occurs almost daily when they have active ovaries. This preliminary study provides the tools necessary for a population-wide assessment of reproduction. We established the time-specific, histological criteria for assessment of spawning rate, and the method was applied to a small sample. A great deal more remains to be done for a proper assessment of reproduction in skipjack tuna. Specifically, many more samples at different times of day, using a

variety of fishing gears, are needed to insure that sampling biases do not exist; a wide range of skipjack tuna sizes or ages need to be sampled so that the age-specific reproductive effort can be estimated; and females with hydrated oocytes need to be collected to verify that nearly all oocytes in the most advanced mode are hydrated and spawned. The last point seems particularly important because our estimated body weight cost of reproduction is high and is very sensitive to the estimate of batch fecundity. It may never be practical to analyze histologically sufficient numbers of specimens to estimate spawning frequency for all months and ages since some spawning occurs the year around (Nishikawa et al. 1985). On the other hand, it may be practical to calibrate the gonosomatic index (GSI) in peak spawning months using histological criteria and to use the GSI as a calibrated index of spawning frequency during months of low spawning frequency. We do not intend to continue this work but we encourage those working on the biology of tunas to include such studies in their research plans.

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LITERATURE CITED

ALHEIT, J., V. H. ALARCON, AND B. J. MACEWICZ.
1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25:43-52.

ARGUE, A. W., F. CONAND, AND D. WHYMAN.
1983. Spatial and temporal distributions of juvenile tunas from the stomachs of tunas caught by pole-and-line gear in the central and western Pacific Ocean. Tuna and Billfish Assessment Programme, Tech. Rep. No. 9, 47 p. South Pacific Commission, Noumea, New Caledonia.

BATTS, B. S.
1972. Sexual maturity, fecundity, and sex ratios of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), in North Carolina waters. Trans. Am. Fish. Soc. 101:627-637.

BRETSCHNEIDER, L. H., AND J. J. DUYVENE DE WIT.
1947. Sexual endocrinology of non-mammalian vertebrates. Monographs on the Progress of Research in Holland During the War, Vol. 11, Elsevier, N.Y., 147 p.

BROCK, V. E.
1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pac. Sci. 8:94-104.

BUÑAG, D. M.
1956. Spawning habits of some Philippine tuna based on diameter measurements of the ovarian ova. Philipp. J. Fish. 4(2):145-177.

CAYRÉ, P.
1981. Maturité sexuelle, fécondité et sex ratio du Listao (*Katsuwonus pelamis*) des côtes d'Afrique de l'ouest (20°N-0°N) étudiés à partir des débarquements thoniers (1977 à 1979) au port de Dakar, (Sénégal). Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 15:135-149.

COCHRAN, W. G.
1977. Sampling techniques. 3d ed. John Wiley & Sons, N.Y., 428 p.

DEMARTINI, E. E., AND R. K. FOUNTAIN.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547-560.

GOLDBERG, S. R., AND D. W. K. AU.
In press. The spawning of skipjack tuna from southeastern Brazil as determined from histological examination of ovaries. *In* P.E. K. Symons, P. M. Miyake, and G. S. Sakagawa (editors), Proceedings of the ICCAT Conference on the International Skipjack Year Program. Int. Comm. Conserv. Atl. Tunas, Madrid, Spain.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

HUNTER, J. R., AND N. C. H. LO, AND R. J. H. LEONG.
1985. Batch fecundity in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), p. 67-78. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

HUNTER, J. R., AND B. J. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.
1985a. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), p. 79-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.
1985b. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:119-136.

ISAAC-NAHUM, V. J., R. DE D. CARDOSO, G. SERVO, AND C. L. DEL B. ROSSI-WONGSCHOWSKI.
1985. Some aspects of the spawning biology of the Brazilian sardine, *Sardinella brasiliensis*, (Clupeidae). International Council for the Exploration of the Sea. C.M. 1985/H:63. Pelagic Fish Comm. 12 p. (Mimeo.)

IVERSON, R. T. B., E. L. NAKAMURA, AND R. M. GOODING.
1970. Courting behavior in skipjack tuna, *Katsuwonus pelamis*. Trans. Am. Fish. Soc. 99:93.

JOSEPH, J.
1963. Fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. 7:255-292.

KAYA, C. M., A. E. DIZON, S. D. HENDRIX, T. K. KAZAMA, AND M. K. K. QUEENTH.
1982. Rapid and spontaneous maturation, ovulation, and

spawning of ova by newly captured skipjack tuna, *Katsuwonus pelamis*. Fish. Bull., U.S. 80:393-396.

LAMBERT, J. G. D.
1970. The ovary of the guppy, *Poecilia reticulata*. The atretic follicle, a *corpus atreticum* or a *Corpus luteum praeovulationis*. Z. Zellforsch 107:54-67.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MATSUMOTO, W. M., R. A. SKILLMAN, AND A. E. DIZON.
1984. Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 451, 92 p. [Also FAO Fisheries Synopsis No. 136.]

NAGANUMA, A.
1979. On spawning activities of skipjack tuna in the western Pacific Ocean. Bull. Tohoku Reg. Fish. Res. Lab. 40:1-13.

NISHIKAWA, Y., M. HONMA, S. UEYANAGI, AND S. KIKAWA.
1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956-1981. Far Seas Fish. Res. Lab. S series 12, 99 p.

PRESENT, T. M. C.
1985. Patterns and processes of energy allocation between growth and reproduction in the marine shore fish, *Hypsoblennius jenkinsi*. Ph.D. Thesis, Univ. California, San Diego, La Jolla, 250 p.

RAJU, G.
1964. Studies on the spawning of the oceanic skipjack *Katsuwonus pelamis* (Linnaeus) in Minicoy waters. *In* Proceedings of the Symposium on Scombroid Fishes, p. 744-768. Mar. Biol. Assoc. India, Symp. Ser. 1.

SCHAEFER, K. M.
1986. Reproductive biology of the black skipjack, *Euthynnus lineatus*. M.S. Thesis, San Diego State Univ., San Diego, CA, 115 p.

SIMMONS, D. C.
1969. Maturity and spawning of skipjack tuna (*Katsuwonus pelamis*) in the Atlantic Ocean, with comments on nematode infestation of the ovaries. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 580, 17 p.

SURVIVAL AND GROWTH OF STRIPED BASS, *MORONE SAXATILIS*, AND *MORONE* HYBRID LARVAE: LABORATORY AND POND ENCLOSURE EXPERIMENTS[1]

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ABSTRACT

Survival and growth of striped bass, *Morone saxatilis*, and its hybrids were compared in the first 30 days after hatching to determine if the reported heterosis of hybrid striped bass is evident in the larval stage. Larvae of striped bass (SB); striped bass × white bass (WBX), *M. saxatilis* ♀ × *M. chrysops* ♂; and striped bass × white perch (WPX), *M. saxatilis* ♀ × *M. americana* ♂, were reared under controlled conditions in the laboratory (19°C, 3‰) and under ambient conditions in freshwater pond enclosures. In the laboratory SB had a significantly higher mean survival rate at 30 days of age than either hybrid. In the pond enclosures neither mean survival nor size at 30 days differed significantly among the types of larvae. Mean rates of growth in length, which ranged from 0.28 to 0.36 mm d^{-1} in the laboratory and from 0.30 to 0.32 mm d^{-1} in the enclosures did not differ significantly among the types of larvae. Mean rates of growth in weight of 15.0 to 19.0% d^{-1} were not significantly different in the laboratory, but the rates did differ significantly in the pond enclosures, where the WBX (17.9% d^{-1}) and WPX (17.3% d^{-1}) rates were significantly higher than the SB (15.5% d^{-1}). If 30-day-old fry were to be reared in hatcheries, there is no clear production advantage for hybrids. A possible initial expression of hybrid vigor, recognized by faster rates of growth in weight, was evident in WBX and WPX at 1 month of age in the pond enclosures but not in the laboratory tanks.

A series of recruitment failures (Cooper and Polgar 1981; Boreman and Austin 1985) has stimulated the development of hatcheries to culture juvenile striped bass, *Morone saxatilis*, or its hybrids for stocking in the Chesapeake Bay region. The striped bass and the striped bass × white bass, *M. chrysops*, hybrid have been cultured for stocking in freshwater and estuarine systems for several years and also have potential for commercial aquaculture (Bonn et al. 1976; Kerby et al. 1983). A second hybrid, striped bass × white perch, *M. americana*, has been produced (Bayless 1972; Kerby and Joseph 1979) although its potential is less known. The striped bass × white bass hybrid demonstrates an apparent heterosis and usually grows and survives better during the first two years of life than does striped bass under similar culture conditions (Logan 1968; Ware 1975; Williams et al. 1981; Kerby et al. 1983).

The objective of our experiments was to determine if the apparent heterosis of the striped bass × white bass hybrid is established in the larval stage, between hatching and 30 d posthatch. We compared growth and survival of striped bass, striped bass × white bass, and striped bass × white perch (referred to hereafter as "striped bass", "white bass hybrid", and "white perch hybrid") in laboratory experiments and in fine-mesh enclosures within hatchery ponds.

METHODS

Laboratory Experiments

Larvae originated from eggs of a single female striped bass, 15.4 kg, gillnetted in the Patuxent River, transported to the Manning Hatchery, Cedarville, MD, on 24 April 1982 and spawned by injection of human chorionic gonadotropin on 27 April. Sperm from 2 male striped bass (Patuxent River), 12 male white bass (Tennessee Fish Commission), and 2 male white perch (Patuxent River) were used to fertilize portions of the spawned eggs. Embryos were incubated in 114 L polyethylene incubation chambers and larvae were held there in 15°-16°C freshwater until 6 d after hatching when some were brought to the Chesapeake Biological Laboratory.

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Rearing Systems

The striped bass and hybrid larvae were reared from 6 to 30 d after hatching in 36 L, rectangular glass aquaria. Each aquarium was lighted by two 61 cm, 40-W fluorescent lights 25 cm overhead on a 12-h light-12-h dark cycle. Immersion heaters controlled the temperature. For additional control, the aquaria sat in a shallow, refrigerated waterbath. An airstone in each aquarium provided oxygen and kept food dispersed.

Temperature was maintained at 19° ± 1°C. Salinity was held at 3‰ by diluting 5 μm filtered Patuxent River water with well water. All larvae were fed *Artemia* nauplii, eggs of which originated from Shark Bay, Australia. Water quality was maintained by replacing half of the water in each aquarium on alternate days. Feces, dead *Artemia*, and dead larvae were siphoned off each day. Ammonia levels were checked on 13 May (16 d after hatching) and were <0.25 ppm in all tanks. The pH in the nine rearing tanks ranged from 8.0 to 8.4 on 11 May (14 d after hatching) and from 8.3 to 8.4 on 26 May (29 d after hatching).

Food Levels, Larval Densities, and Sampling

Two *Artemia* nauplii levels, 100 L^{-1} and 500 L^{-1}, were tested. The lower level is similar to zooplankton densities in Chesapeake Bay subestuaries where striped bass larvae occur (Miller 1978). For each of the larval types duplicate experiments were run at the 500 L^{-1} level but only a single experiment was run at 100 L^{-1}. Food was first offered at 6 d after hatching when the experiments started. *Artemia* nauplii concentrations in each aquarium were checked twice daily by counting the number in pipetted 100 cc aliquots. Food levels were maintained and adjusted by adding suspensions of *Artemia* of known concentration to the aquaria.

In each aquarium, 144 larvae were stocked at an initial, relatively low density of 4.0 L^{-1}. Some larvae were preserved in 5% Formalin[4] at the start of experiments (6 d after hatching). Three or four larvae from each aquarium were sampled and preserved on days 8, 10, 13, 16, 19, and 25 for growth rate determination. Samples (15-27 larvae) of survivors were preserved at 30 d when experiments were terminated. Preserved larvae were measured and wet-weighed (nearest 0.1 mg after blotting).

Analysis

The expected number of survivors in each experiment is the number that would have survived had no larvae been sampled and preserved during the experiments. If $Z = F + M$, where Z is instantaneous total mortality and F is preservation mortality, then M is mortality from all other causes. The expression $N_t = N_0\, e^{-(F+M)t}$ applies, where N_t is number of survivors at age t (30 d) and N_0 is initial number of stocked larvae (144 at 6 d). Knowing N_0, N_t, Z, and F, we solved for M and then estimated expected survivors, if no larvae had been preserved, as $N'_t = N_0\, e^{-Mt}$. Analysis of variance was used to test for survival differences among types of larvae and between food levels.

Lengths and weights of the three types of larvae were compared at 6 d after hatching and when experiments terminated. In addition, lengths and weights at the 100 L^{-1} and 500 L^{-1} food levels were compared to determine if food concentration affected mean sizes. Comparisons were carried out using analysis of variance followed by the SNK multiple comparison test.

Growth in length was described by linear regressions of standard length on days after hatching, $l_t = a + bt$, where l_t is estimated length (mm) at age t and b is daily growth rate (mm day^{-1}). Growth in weight was determined from the exponential regression of wet weight (mg) on days after hatching, $W_t = W_0\, e^{Gt}$, where W_t is estimated weight at age t and G is the instantaneous daily growth coefficient (day^{-1}). Percent daily weight gains were calculated as 100 ($e^G - 1$). Weight-length relationships were obtained from the power function, $W = aL^b$, where W is wet weight (mg), l is standard length (mm), and a and b are coefficients from the fitted regression.

Enclosure Experiments

Cubic enclosures, 1.32 m on each side, open at the top, and constructed of wood frames and 500 μm Nitex mesh, were submerged to a depth of 1.12 m in a 1-acre, freshwater pond of 1.5 m mean depth at the Manning Hatchery. The nine enclosures, each holding 2 m^3, were placed in the pond from 3 to 5 d before larvae were stocked. Enclosures were assigned to the striped bass and two hybrids using a linearized Latin-square design (Steel and Torrie 1960) with three replicates for each type of larva. The larvae were progeny of a single 10.4 kg female

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

striped bass from the Patuxent River. Sperm from Patuxent River male striped bass were used to fertilize eggs. The hybrids resulted from fertilization by Tennessee white bass males and Patuxent River white perch males.

Larvae were held in hatchery troughs and fed *Artemia* nauplii from 6 to 8 d after hatching. A total of 2,500 9-d-old larvae were stocked in each enclosure on 12 May 1983. Larvae were sampled by dipnet and preserved in 5% Formalin at 13, 17, 20, 23, and 27 d after hatching. At 30 d all survivors from each enclosure were counted and samples preserved. Temperatures in the pond ranged from 18.5° to 22.0°C during the course of the experiment.

Pond Zooplankton

The kinds and abundances of potentially edible zooplankton were sampled on each day that larvae were collected, using a 15 cm diameter, 72 μm mesh plankton net that was lifted vertically in each enclosure. For comparison, zooplankton also was collected in three vertical lifts of the net outside the enclosures.

Analysis

Survival, lengths and weights at age, growth rates, and weight-length relationships were calculated as for the laboratory experiments. Variance, covariance, and regression analyses were used to test for differences in means among the striped bass and two types of hybrid larvae.

RESULTS

Laboratory Experiments

Survival

Survival at 30 d after hatching ranged from 45.8 to 85.4% (Table 1). Mean percentage survivals were striped bass, 84.7%; white bass hybrid, 60.4%; and white perch hybrid, 73.1%. The mean expected number of survivors differed significantly among types of larvae (ANOVA, $P < 0.05$). Mean survival of striped bass was significantly higher than that of the white bass hybrids (SNK multiple comparison procedure, $P < 0.05$). There were no detectable differences in mean survival between the two *Artemia* nauplii feeding levels (ANOVA, $P > 0.05$).

Size-at-Age

The white perch hybrid larvae were significantly shorter and weighed less than either striped bass or white bass hybrid larvae when the experiments began at 6 d after hatching, before larvae had been fed (Table 2; ANOVA, $P < 0.05$).

At 30 d after hatching there were some statistically significant differences in mean lengths and weights among the three types of larvae, and between the two food levels, but no clear result was obtained (Table 2). No significant differences among mean lengths or weights of the white bass hybrid larvae were detected between the 100 L^{-1} and 500 L^{-1} food levels. But, the striped bass and white

TABLE 1.—Survival at 30 d after hatching of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) larvae in laboratory experiments at two food levels.

Larvae and experiment numbers	*Artemia* concentration (number L^{-1})	Number preserved	Number of survivors	Expected number[1] of survivors	Expected instantaneous daily mortality rates (Z)	Expected percentage survival
SB-1	500	20	106	123	0.0066	85.4
SB-2	500	18	108	123	0.0066	85.4
SB-3	100	19	104	122	0.0069	83.3
SB mean			106.0	[2]122.0	0.0069	84.7
WBX-1	500	18	58	66	0.0325	45.8
WBX-2	500	20	93	108	0.0120	75.0
WBX-3	100	18	76	87	0.0210	60.4
WBX mean			75.7	87.0	0.0210	60.4
WPX-1	500	22	85	100	0.0152	69.4
WPX-2	500	18	100	114	0.0097	79.2
WPX-3	100	18	89	102	0.0144	70.8
WPX mean			91.3	105.3	0.0130	73.1

[1]Expected number of survivors is the adjusted number, accounting for samples of larvae that were preserved during the experiment (see Methods).

[2]The SB mean differed significantly from the WBX and WPX means (Analysis of variance followed by SNK multiple comparison procedure, $P < 0.05$).

TABLE 2.—Mean standard lengths and wet weights of larvae of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) from specimens preserved at 6 d after hatching, immediately before the experiments began and at 30 d after hatching when the experiments were terminated.

SIX DAYS

Larvae	Number preserved	Mean length (mm) and standard error $\bar{x}$	$s_{\bar{x}}$	Mean wet weight (mg) and standard error $\bar{x}$	$s_{\bar{x}}$
SB	15	5.49	0.06	0.95	0.04
WBX	19	5.29	0.03	0.96	0.03
WPX	17	[1]5.20	0.06	[1]0.85	0.02

THIRTY DAYS

Larvae and experiment number	*Artemia* concentration (number L^{-1})	Number preserved	Mean length (mm) and standard error $\bar{x}$	$s_{\bar{x}}$	Mean wet weight (mg) and standard error $\bar{x}$	$s_{\bar{x}}$
SB-3	100	18	[2]12.39	0.17	[2]25.7	1.4
SB-1	500	20	[3]14.26	0.17	[4]49.1	2.2
SB-2	500	19	[3]14.57	0.17	[4]50.4	1.8
SB mean			13.74		41.7	
WBX-3	100	15	13.02	0.30	30.1	2.1
WBX-1	500	18	12.68	0.26	28.8	2.2
WBX-2	500	19	12.73	0.38	29.3	3.6
WBX mean			12.81		29.4	
WPX-3	100	21	[2]11.86	0.25	[2]21.1	1.6
WPX-1	500	18	13.22	0.31	33.6	2.2
WPX-2	500	27	13.15	0.22	35.0	2.2
WPX mean			12.74		29.9	

[1]Differ significantly, $P < 0.05$, from both SB and WBX. ANOVA followed by SNK multiple comparison procedure.
[2]Differ significantly, $P < 0.05$, from the 500 L^{-1} means. ANOVA.
[3]Differ significantly, $P < 0.05$, from all WBX and WPX mean lengths. ANOVA followed by SNK multiple comparison procedure.
[4]Differ significantly, $P < 0.05$, from all WBX and WPX mean weights. ANOVA followed by SNK multiple comparison procedure.

perch hybrid larvae were longer and heavier at the 500 L^{-1} level (ANOVA, $P < 0.05$). At the 500 L^{-1} food level the striped bass were significantly heavier than either hybrid (ANOVA and SNK multiple comparison procedure, $P < 0.05$). The mean lengths of 30-d-old striped bass at 500 L^{-1} food level were significantly longer than the mean lengths of the hybrids (Table 2) (ANOVA and SNK multiple comparison procedure, $P < 0.05$).

Growth Rates

From 6 to 30 d after hatching larvae grew in length at mean rates ranging from 0.28 to 0.36 mm d^{-1} (Table 3, Fig. 1). There were no significant differences in the growth-in-length rates among the three types of larvae at the 500 L^{-1} *Artemia* food level.

The exponential regressions of mean weights on age (Table 3, Fig. 2) gave instantaneous growth coefficients ranging from 0.1396 to 0.1739 d^{-1}, equivalent to 15-19% d^{-1} weight gains. None of the coefficients differed significantly from each other (ANCOVA, $P > 0.50$).

There were no significant differences in weight-length relationships among types of larvae or between food levels (ANCOVA, $P > 0.50$). An average relationship, based on the total regression component of the ANCOVA, is $W = 7.17 \times 10^{-4}\, l^{4.2399}$.

Enclosure Experiments

Survival

Survival of striped bass and hybrid larvae at 30 d after hatching ranged from 13.1 to 33.8% in the nine enclosures. At 30 d there was no indication that striped bass or either hybrid was superior in survival capability. The mean percentage survivals for the three types of larvae ranged from 22.0 to 28.5% (Table 4B) and did not differ significantly (ANOVA on arcsin mean percent survivals). The mean overall survival rate for the three kinds of larvae was 25.0%.

TABLE 3.—Linear regressions describing growth in length and exponential regressions describing growth in weight of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) during the period 6-30 d after hatching. In the linear regression, l is standard length in mm, t equals days after hatching, b equals growth rate in mm, and a is the y-axis intercept. In the exponential regressions, W is wet weight in mg, t equals days after hatching, G is the instantaneous growth coefficient, and W_0 is the theoretical weight in mg at time zero.

LENGTH

Larvae and experiment number	*Artemia* concentration (number L^{-1})	Equation $l = a + bt$	Standard error of b	r^2
SB-3	100	[1] $l = 3.64 + 0.29t$	0.01	0.99
SB-1	500	$l = 3.13 + 0.36t$	0.02	0.99
SB-2	500	$l = 3.20 + 0.36t$	0.01	0.99
WBX-3	100	$l = 3.10 + 0.34t$	0.02	0.98
WBX-1	500	$l = 3.36 + 0.32t$	0.01	0.99
WBX-2	500	$l = 3.31 + 0.32t$	0.02	0.98
WPX-3	100	[1] $l = 3.70 + 0.28t$	0.02	0.98
WPX-1	500	$l = 3.18 + 0.32t$	0.01	0.99
WPX-2	500	$l = 3.22 + 0.32t$	0.01	0.99

WEIGHT

Larvae and experiment number	*Artemia* concentration (number L^{-1})	Equation $W = W_0 e^{Gt}$	Standard error of G	r^2	Percent gain (% d^{-1})
SB-3	100	$W = 0.51\ e^{0.1472t}$	0.0158	0.94	15.9
SB-1	500	$W = 0.41\ e^{0.1713t}$	0.0141	0.96	18.7
SB-2	500	$W = 0.42\ e^{0.1739t}$	0.0146	0.96	19.0
WBX-3	100	$W = 0.41\ e^{0.1581t}$	0.0147	0.95	17.1
WBX-1	500	$W = 0.41\ e^{0.1576t}$	0.0145	0.95	17.1
WBX-2	500	$W = 0.31\ e^{0.1645t}$	0.0154	0.95	17.9
WPX-3	100	$W = 0.48\ e^{0.1396t}$	0.0123	0.96	15.0
WPX-1	500	$W = 0.33\ e^{0.1625t}$	0.0073	0.96	17.6
WPX-2	500	$W = 0.35\ e^{0.1520t}$	0.0091	0.98	16.4

[1]Differ significantly from SB-1 and SB-2, $P < 0.01$. ANCOVA followed by SNK multiple comparison procedure.

The mean instantaneous mortality rates during the 9-30 d after hatching ranged from 0.0601 to 0.0713 d^{-1}, equivalent to 5.8 to 6.9% d^{-1} (Table 4B). Cannibalism probably occurred during the last 10 d of the experiment. Some large survivors had small larvae in their stomachs when the experiments ended.

Size-at-Age

When larvae were stocked in the enclosures at 9 d after hatching, white bass hybrid larvae were significantly heavier (ANOVA, $P < 0.01$) and slightly, but not significantly, longer than white perch hybrid and striped bass larvae (Table 4A). Because all larvae had been fed *Artemia* nauplii in the hatchery for 3 d prior to stocking it is not known if the sizes at stocking reflect the relative weights and lengths of the three kinds of larvae before they began to feed.

At 30 d after hatching mean lengths of striped bass and hybrid larvae from the enclosures ranged from 12.58 to 12.96 mm SL (Table 4C). Mean wet weights ranged from 38.38 to 43.28 mg (Table 4C). There were no significant differences in mean lengths or weights among the three types of larvae or among the nine enclosures (ANOVA, $P > 0.25$).

Growth Rates

Mean rates of growth in length for the striped bass and hybrid larvae ranged from 0.30 to 0.32 mm d^{-1} (Table 4D; Fig. 3). There were no significant differences in the rates among types of larvae or among replicate enclosures (ANCOVA, $P > 0.10$).

The common, instantaneous rates of growth in weight were 0.1444 for striped bass (= 15.5% d^{-1}), 0.1650 for white bass hybrids (= 17.9% d^{-1}) and 0.1593 for white perch hybrids (= 17.3% d^{-1}). The rates of growth (Table 4E; Fig. 4) differed significantly among the three types of larvae (ANCOVA, $P < 0.05$) but not among enclosures ($P > 0.10$). The

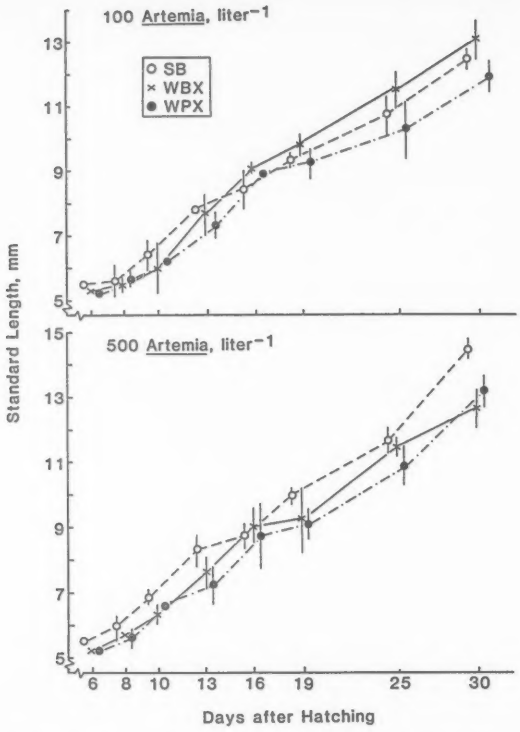

FIGURE 1.—Mean standard lengths ±2 standard errors of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) larvae from 6 to 30 d after hatching, reared at two food levels in the laboratory.

white bass hybrid and white perch hybrid rates were significantly higher than that for striped bass larvae (SNK multiple comparison procedure, $P < 0.05$).

Weight-Length Relationships

The wet weight-standard length relationships differed significantly among the three types of larvae (ANCOVA, $P < 0.001$). The power coefficient of the white bass hybrid larvae was higher than those of the striped bass and white perch hybrid larvae (SNK multiple comparison test, $P < 0.01$) (Table 4F).

Pond Zooplankton

Copepod nauplii and adults (*Diaptomus* spp. and other calanoid species) and cladocerans (*Bosmina*, *Scapholebris*, *Ceriodaphnia*, and *Daphnia*) were abundant in the pond and in the enclosures (Fig. 5). The summed cladoceran and copepod densities declined rapidly in the pond from >1,000 L^{-1}, when the larvae were stocked, to approximately 400 L^{-1} during the last 10 d of the experiment. Densities within the enclosures declined from approximately 1,000 L^{-1} at the time larvae were stocked to 100 L^{-1} when the experiments ended.

Samples of 12-20 larvae of each type were examined for stomach contents on day 30. The smallest larvae of each type had eaten cladocerans and copepods. The largest individuals had eaten chironomid larvae and zooplankton. Two of 20 individuals of striped bass and white bass hybrids had eaten fish larvae, proof that cannibalism was occurring.

DISCUSSION

Neither striped bass nor hybrid larvae, in the lab-

TABLE 4.—Summary of data and analyses from 2 m^3 enclosure experiments in the Manning Hatchery pond, 1983. Three replicate enclosures were run for each type of larva: Striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX). A) Mean standard lengths and wet weights at 9 d after hatching, prior to stocking in enclosures. B) Percent survivals at 30 d after hatching. C) Mean lengths and weights at 30 d after hatching. D) Growth-in-length equations (l_t = standard length in mm at age t; t = days after hatching; S_b = standard error of the regression coefficient; r^2 = coefficient of determination). E) Exponential, growth-in-weight equations (W_t = wet weight in mg at age t; t = days after hatching; S_G = standard error of the exponential coefficient; r^2 = coefficient of determination). F) Power function equations of the wet weight-standard length relationships (W = wet weight in mg; l = standard length in mm; S_b = standard error of the power coefficient; r^2 = coefficient of determination).

A.

Type of larva	n	Standard length (mm) $\bar{x}$	$s_{\bar{x}}$	Wet weight (mg) $\bar{x}$	$s_{\bar{x}}$
SB	13	6.12	0.06	1.15	0.08
WBX	13	6.19	0.14	[1]1.66	0.11
WPX	15	5.87	0.13	1.33	0.11

B.

Type of larva	Percent survival $\bar{x}$	$s_{\bar{x}}$	Instantaneous mortality rate (d^{-1})
SB	22.1	3.4	0.0713
WBX	22.0	6.2	0.0695
WPX	28.5	2.1	0.0601

C.

Type of larva	n	Standard length (mm) $\bar{x}$	$s_{\bar{x}}$	Wet weight (mg) $\bar{x}$	$s_{\bar{x}}$
SB	78	12.58	0.24	38.38	3.57
WBX	78	12.90	0.23	43.28	3.86
WPX	78	12.96	0.12	39.73	1.23

D.

Type of larva	Equation $l_t = a + bt$	n	S_b	r^2
SB	$l_t = 3.09 + 0.30t$	253	0.0136	0.66
WBX	$l_t = 3.22 + 0.31t$	245	0.0130	0.70
WPX	$l_t = 2.96 + 0.32t$	263	0.0100	0.79

E.

Type of larva	Equation $W_t = W_0 e^{Gt}$	n	S_G	r^2
SB	$W_t = 0.37\, e^{0.1444t}$	253	0.0044	0.81
WBX	[2]$W_t = 0.26\, e^{0.1650t}$	245	0.0041	0.87
WPX	[2]$W_t = 0.30\, e^{0.1593t}$	263	0.0037	0.88

F.

Type of larva	Equation $W = al^b$	n	S_b	r^2
SB	$W = 6.23 \times 10^{-4} L^{4.2879}$	253	0.0469	0.97
WBX	[3]$W = 2.27 \times 10^{-4} L^{4.7114}$	245	0.0536	0.97
WPX	$W = 5.44 \times 10^{-4} L^{4.3496}$	263	0.0512	0.97

[1]Significant at $P < 0.05$. ANOVA.
[2]The WBX and WPX exponential coefficients differed significantly, $P < 0.05$, from the SB coefficient. ANCOVA followed by SNK multiple comparison procedure.
[3]The WBX power coefficient differed significantly, $P < 0.05$, from the SB and WPX coefficients. ANCOVA followed by SNK multiple comparison procedure.

oratory and in freshwater pond enclosures, demonstrated clearly superior growth or survival. The apparent heterosis in young-of-the-year and subadult white bass hybrids (Logan 1968; Ware 1975; Bonn et al. 1976; Williams et al. 1981; Kerby et al. 1983) was not evident during the first month after hatching. Survival and growth rates of the three types of larvae were relatively high in all of our experiments, indicating that striped bass and its hybrids may have near-equal production potential up to 30 d of age.

Larvae grew and survived surprisingly well at the relatively low food concentrations that we offered in the laboratory. There was evidence that striped bass and white perch hybrid larvae grew faster at the 500 L^{-1} than at the 100 L^{-1} *Artemia* concentration but there was no significant difference in size of white bass hybrid larvae reared at those two food levels. Survival of all three types of larvae did not differ between the two food levels, demonstrating that high survival and favorable growth can be ob-

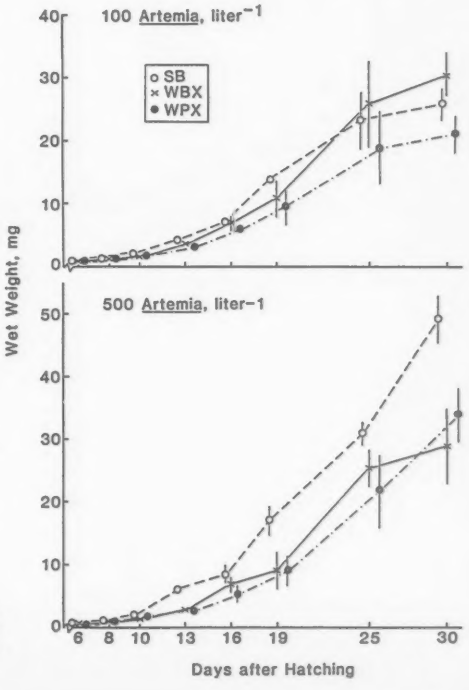

FIGURE 2.—Mean wet weights ±2 standard errors of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) larvae from 6 to 30 d after hatching, reared at two food levels in the laboratory.

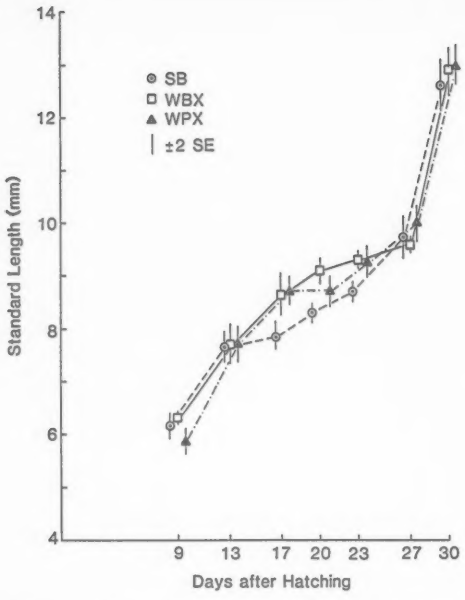

FIGURE 3.—Mean standard lengths (±2 standard errors) of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) larvae on seven dates in 2 m^3 enclosure experiments, Manning Hatchery pond.

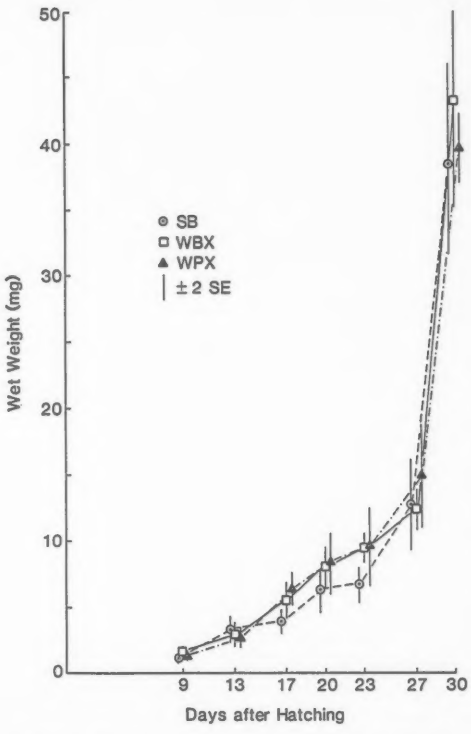

FIGURE 4.—Mean wet weights (±2 standard errors) of striped bass (SB), striped bass × white bass (WBX), and striped bass × white perch (WPX) larvae on seven dates in 2 m^3 enclosure experiments, Manning Hatchery pond.

tained for *Morone* larvae at low *Artemia* concentrations, if those concentrations are maintained at the nominal levels. Our laboratory survival rates at low food levels were higher than those reported for striped bass larvae in the literature (e.g., Doroshev 1970; Miller 1978; Rogers and Westin 1981; Eldridge et al. 1981, 1982), which generally had indicated that nominal *Artemia* concentrations nearly an order of magnitude higher than 500 L^{-1} were required to obtain high survival rates.

The laboratory and pond enclosure methods to assess striped bass and hybrid larvae performance differed in many respects and could have influenced results. Besides great differences in enclosed volumes (36 L vs. 2 m^3), environmental factors and foods differed. Laboratory experiments were run at 19.0°C and 3‰ salinity, because low salinities are known to improve striped bass larvae survival (Bonn et al. 1976; Kerby et al. 1983). Temperature increased from 18.5° to 22.5°C in the Manning Hatchery freshwater pond during the 3-wk experiment. The laboratory-reared fish were fed only *Artemia* nauplii at controlled concentrations while enclosure fish had a variable zooplankton diet.

Survival of all larvae was lower in the pond enclosures than in the laboratory tanks (Tables 1, 4). White bass hybrids had the lowest mean survival rate in the laboratory but they survived as well as striped bass and white perch hybrids in the pond enclosures. At the relatively high 500 L^{-1} *Artemia* level laboratory-reared striped bass larvae were longer and heavier than either of the hybrids at 30 d after hatching. In the pond enclosures no significant differences in mean lengths or weights among the three types of larvae were detected at 30 d. The weight-length relationship of pond enclosure, white bass hybrid larvae had a relatively high exponential coefficient, indicating that they were heavier at a given length than the other types of larvae. Mean weights of both hybrids at 30 d were considerably heavier in the pond enclosures than in the laboratory tanks. Relatively great size variability in the

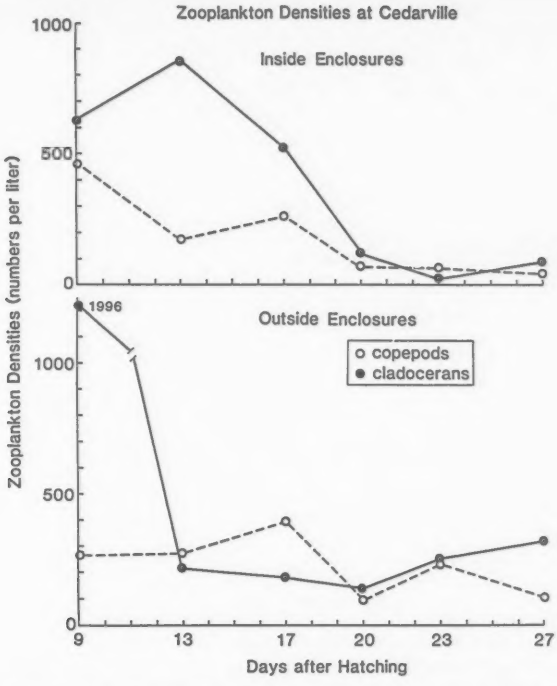

FIGURE 5.—Mean densities of copepods and cladocerans inside and outside of the 2 m^3 enclosures used for striped bass and hybrid larvae experiments in the Manning Hatchery pond.

enclosures may have resulted in part from cannibalism and consumption of chironomids by some larvae, promoting their relatively rapid growth.

Although mean weights and lengths of 30-d-old striped bass and the two hybrids from the pond enclosures did not differ, the instantaneous rate of growth in weight of striped bass larvae was significantly lower than that of either hybrid (Table 4E). Had the enclosure experiments proceeded for a few more days the hybrids would have attained larger size than the striped bass. For example, at 35 d after hatching the striped bass would have weighed 20 mg less than either hybrid. The heterotic effect may begin to express itself at approximately 1 mo of age. Alternatively, the freshwater environment, increasing temperatures, and the prey available in the pond may have selectively favored growth of hybrids during the last few days of the experiment.

If 30-d-old fry are to be produced for stocking, there is no apparent immediate advantage to rear hybrids rather than striped bass. Our laboratory and pond enclosure studies did not demonstrate advantages in survival or production of hybrids. The pond enclosure results did suggest that hybrids may begin to achieve an advantage in growth rates just prior to 1 mo of age. Important questions about comparative energetics, nutrition, and genetics still remain to be answered to understand the biology of larval *M. saxatilis* or its hybrids and the consequences of their possible release into natural systems such as Chesapeake Bay.

ACKNOWLEDGMENTS

The research was supported by contracts F26-82-003 and F31-83-008 from the Maryland Department of Natural Resources, Tidewater Administration, Tidal Fisheries Division. Assistance in the laboratory was provided by H. Hornick, W. Roosenburg, and V. Saksena. Larvae were supplied by the Maryland DNR Manning Hatchery at Cedarville. The assistance of DNR personnel, particularly M. Beaven, H. King, and J. Stringer, is gratefully acknowledged. We appreciate the critiques of early

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LITERATURE CITED

BAYLESS, J. D.
1972. Artificial propagation and hybridization of striped bass, *Morone saxatilis* (Walbaum). South Carolina Wildl. Mar. Resour. Dep., 135 p.

BONN, E. W., W. M. BAILEY, J. C. BAYLESS, K. E. ERICKSON, AND R. E. STEVENS.
1976. Guidelines for striped bass culture. Southern Div., Am. Fish. Soc., 103 p. plus app.

BOREMAN, J., AND H. M. AUSTIN.
1985. Production and harvest of anadromous striped bass stocks along the Atlantic coast. Trans. Am. Fish. Soc. 114:3-7.

COOPER, J. C., AND T. T. POLGAR.
1981. Recognition of year-class dominance in striped bass management. Trans. Am. Fish. Soc. 110:180-187.

DOROSHEV, S. I.
1970. Biological features of the eggs, larvae and young of the striped bass [*Roccus saxatilis* (Walbaum)] in connection with the problem of its acclimatization in the USSR. J. Ichthyol. 10:235-248.

ELDRIDGE, M. B., J. A. WHIPPLE, AND M. J. BOWERS.
1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. Fish. Bull., U.S. 80:461-474.

ELDRIDGE, M. B., J. A. WHIPPLE, D. ENG, M. J. BOWERS, AND B. M. JARVIS.
1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Trans. Am. Fish. Soc. 110: 111-120.

KERBY, J. H., AND E. B. JOSEPH.
1979. Growth and survival of striped bass and striped bass × white perch hybrids. Proc. Annu. Conf. Southeastern Assoc. Fish Wildl. Agencies 32:715-726.

KERBY, J. H., L. C. WOODS III, AND M. T. HUISH.
1983. Culture of the striped bass and its hybrids: A review of methods, advances and problems. *In* R. F. Stickney and S. P. Meyers (editors), Proceedings of the Warmwater Fish Culture Workshop, p. 23-54. World Maricult. Soc., Spec. Publ. 3.

LOGAN, H. J.
1968. Comparison of growth and survival rates of striped bass and striped bass × white bass hybrids under controlled environments. Proc. Annu. Conf. Southeast Assoc. Fish Game Comm. 21:260-263.

MILLER, P. E.
1978. Food habit study of striped bass post yolk-sac larvae. Johns Hopkins Univ., Chesapeake Bay Inst., Spec. Rep. 68, 49 p.

ROGERS, B. A., AND D. T. WESTIN.
1981. Laboratory studies on effects of temperature and delayed initial feeding on development of striped bass larvae. Trans. Am. Fish. Soc. 110:100-110.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., N.Y., 481 p.

WARE, F. J.
1975. Progress with *Morone* hybrids in fresh water. Proc. Annu. Conf. Southeast Assoc. Fish Game Comm. 28:48-54.

WILLIAMS, J. E., P. A. SANDIFER, AND J. M. LINDBERGH.
1981. Net-pen culture of striped bass × white bass hybrids in estuarine waters of South Carolina: a pilot study. J. World Maricult. Soc. 12:98-110.

ASPECTS OF THE REPRODUCTIVE BIOLOGY, SPATIAL DISTRIBUTION, GROWTH, AND MORTALITY OF THE DEEPWATER CARIDEAN SHRIMP, *HETEROCARPUS LAEVIGATUS*, IN HAWAII

MURRAY D. DAILEY[1] AND STEPHEN RALSTON[2]

ABSTRACT

The recent rapid development of fisheries for the *Heterocarpus laevigatus* in Hawaii and elsewhere in the tropical Pacific has created the need for biological information to manage the resource. This study reports on a 16-month sampling program of commercial shrimp catches in Hawaii, during which the depth of capture, carapace length (CL), sex, and reproductive condition of 7,368 *H. laevigatus* were determined.

The overall sex ratio of *H. laevigatus* was 1:1.16 in favor of females and depended on the depth sampled; there were relatively fewer females as depth increased. Seasonal variation in sex ratio was evident which may have been due to changing catchability and availability or a sex related dispersion pattern. Sex ratio also depended on size category, displaying a standard pattern with no evidence of protandry.

Females mature at 40 mm CL (64% of asymptotic length) and ovigerous individuals are found year round. However, the main reproductive season is from August-February, with over 50% of females carrying eggs from October-January. Mature shrimp may undergo a depth related seasonal migration in synchrony with breeding. Mature males and females were found deeper (700 m) during the reproductive season than not (550 m). Females apparently settle in deep water and migrate gradually to shallower water as they grow.

Seasonal length-frequency data suggest *H. laevigatus* is not semelparous. Separate analyses of CL-frequency distributions of male and female shrimp indicate their von Bertalanffy asymptotic sizes are 57.9 and 62.5 mm CL, respectively. Growth coefficients (K) estimated by modal progression were 0.35 and 0.25 per year for males and females, and total instantaneous mortality rates were 1.51 and 0.73 per year, respectively.

The deepwater caridean shrimp, also known as "ono" or smooth nylon shrimp, *Heterocarpus laevigatus*, (Family Pandalidae) occurs throughout the tropical Pacific Ocean, where it is found in benthic deepwater habitats (450-900 m) (Wilder 1977; King 1983). While early trapping surveys in the Hawaiian Islands revealed its local abundance (Clarke 1972; Struhsaker and Aasted 1974), little information was available concerning its biology. These early studies did show, however, that *H. laevigatus* was potentially of commercial importance, with a preliminary maximum sustained yield estimate of 454-907 metric tons (t) derived for the Hawaiian Archipelago (Department of Land and Natural Resources 1979). More recently the Western Pacific Regional Fishery Management Council[3] (WPRFMC) has revised this estimate to 400-4,000 t.

A commercial trap fishery for this species subsequently developed in the Hawaiian Islands, and in 1984 the WPRFMC began the process of developing a fishery management plan for the *Heterocarpus* shrimp resources of the region. Landings from the Hawaiian fishery exceeded 135 t in 1983 but have declined sharply since, although commercial interest in the resource remains great (WPRFMC fn. 3). Recent research surveys in Hawaii have now more clearly defined this species' depth, temporal, and geographic distributions (Oishi 1983; Hawaiian Divers 1983[4]; Gooding 1984), although the life history of *H. laevigatus* remains largely unknown. The only substantive biological studies to date were

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Manuscript accepted July 1986.
FISHERY BULLETIN: VOL. 84, NO. 4, 1986.

[3]Western Pacific Regional Fishery Management Council. 1984. Status of fisheries assessment of development and management needs for selected crustacean species in the western Pacific region. Unpubl. manuscr., 60 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[4]Hawaiian Divers. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, National Marine Fisheries Service, NOAA, Honolulu, HI, 47 p.

completed in the Marianas (including Guam) and Fiji (Wilder 1977; King 1983; King and Butler 1985; Moffitt and Polovina[5]).

Evidence also exists to show that this species is highly susceptible to trapping (Ralston 1986) and, according to commercial fishermen, depletion of the resource has occurred over certain fishing grounds in Hawaii (S. Barrows[6]). Because estimates of the shrimp's productive capacity which are currently available are preliminary at best and a fishery has developed rapidly, this study set out to examine aspects of the life history of the Hawaiian stock of *H. laevigatus* to obtain information useful in developing a basis for management of the fishery.

METHODS

All sampling was conducted by commercial fishing vessels owned by the Hawaiian Shrimp Company (*Easy Rider*, *Mokihana*, and the *Easy Rider Too*) over the 16-mo period from August 1983 to November 1984. During this time, six 35-60 d cruises were completed and samples were obtained during 9 of the 12 calendar months (Table 1). Fishing was conducted throughout much of the Hawaiian Archipelago, from Gardner Pinnacles south to the Island of Hawaii (Fig. 1). Samples were collected at all of the seven main islands (Hawaii, Kauai, Lanai, Maui, Molokai, Niihau, and Oahu) and from Necker, French Frigate Shoals, and Gardner Pinnacles in the Northwestern Hawaiian Islands.

All shrimp were caught during overnight sets of baited pyramidal traps, which measured 1.5 × 1.8 m with a funnel opening at the top center. Fishing was targeted between depths of 500 and 700 m, although some catches were made in both shallower and deeper water because of the trap drift. The best catch rates were found in areas of hard rough bottom; otherwise, all sampling sites were to all appearances similar.

Systematic subsamples of the catch were taken from every other trap on every second fishing day by randomly scooping approximately 0.9 kg (2 lb) of shrimp from traps prior to emptying. Samples were placed in double bags with tags recording date, location, depth, and condition, and were then frozen and packed for transfer to the laboratory. There all shrimp were identified to species; sexed; examined for embryos on the pleopods; measured to the nearest 0.1 mm for carapace length (CL), carapace width (CW), and total length (TL); and weighed to the nearest 0.1 g on a top loading scale. The data were then keypunched and stored for analysis.

Size-frequency distributions of *H. laevigatus* were analyzed by the regression method of Wetherall et al. (in press) to estimate maximum size (L_∞ of the von Bertalanffy growth equation) and the ratio of total instantaneous mortality rate (Z) to von Bertalanffy growth coefficient (K). Additionally, the growth coefficient of *H. laevigatus* was estimated by following the progression of size modes evident in three large samples taken: 1) 24 October to 6 November 1983, 2) 24 April to 11 May 1984, and 3) 3 September to 6 November 1984. Sample sizes of N = 2,021, 1,991, and 1,438 were obtained in these respective samples, accounting for 74% of all shrimp measured in the study. Modal progression of size distributions was determined by the ELEFAN I computer program of Pauly (1982).

RESULTS

A total of 7,368 *H. laevigatus* were measured and examined for CL, sex, and the presence of eggs (Table 1). Of these 3,956 were females (32.6% of which were ovigerous) and 3,412 were males. This corresponds to an overall male to female sex ratio of 1:1.16, departing significantly from equality ($P < 0.0001$). Measurements of TL, CW, and weight were obtained from 5,920 of the shrimp sampled.

Due to an imbalance in sampling, the effects of location and time on the distribution of *H. laevigatus* could not be completely separated. We therefore assume that all samples were drawn from statistically homogeneous locations in order to isolate and examine temporal and depth effects. The strength of this assumption is based largely on our personal observations and those of fishermen that seasonal change seems to account for most major population

[5]Moffitt, R. B., and J. J. Polovina. The distribution and yield assessment of the deepwater shrimp resource in the Marianas. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[6]S. Barrows, Hawaiian Shrimp Company, 737 Bishop Street, Suite 2910, Honolulu, HI 96813, pers. commun. 1985.

TABLE 1.—Temporal and geographic distribution of *Heterocarpus laevigatus* samples (FFS = French Frigate Shoals).

Year	Month	Location	Sample size
1983	Aug.	Oahu	79
1983	Sept.	Oahu	26
1983	Oct.	FFS	188
1983	Nov.	FFS	1,942
1984	Jan.	Oahu	285
1984	Mar.	Niihau, Kauai	530
1984	April	Hawaii	631
1984	May	Lanai, Maui, Molokai	1,389
1984	June	Necker	842
1984	Sept.	Gardner Pinnacles, FFS, Necker	1,438
1984	Nov.	Necker	18

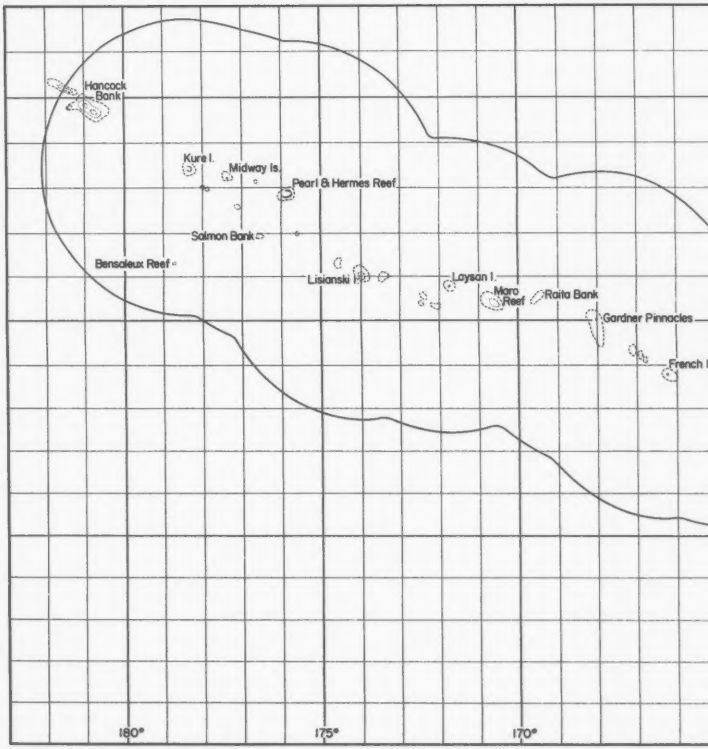
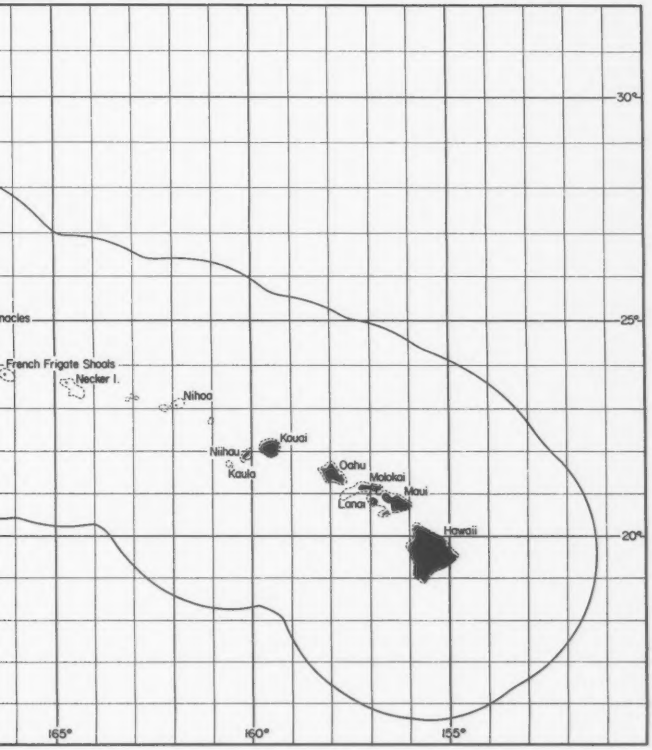


FIGURE 1.—Map of the Hawaiian Archipelago showing sampling locations. Note that the circ
of latitude equals 1



he circumscribed area delimits the U.S. fishery conservation zone and that one degree
quals 111 km.

variations in Hawaii, as well as evidence from the Mariana Archipelago which shows that populations of *H. laevigatus* are affected to a greater degree by temporal factors than geographic ones (Polovina[7]).

Morphometrics

The results of performing functional regressions (Ricker 1973) on the three linear size measurements (CL, CW, TL) are given in Table 2. Estimates of slope and intercept are provided for all possible permutations of these variables. Separate analyses for males (M), females without eggs (FØ), and females with eggs (FE) were not performed because all have similar gross morphologies (but see King and Moffitt 1984). As expected, the data were well described with a linear fit.

The relationship between weight and CL was examined by analysis of covariance (BMDP 1977) to determine whether the M, FØ, and FE subgroups have different weight-length relationships. Results showed all three were characterized by differing slopes in the regression of $\log_e$ (weight) on $\log_e$ (CL) ($F = 86.46$, df = 2, 5912, $P << 0.0001$). Parameter estimates with standard errors and other regression statistics are presented in Table 3 for each of the three subgroups. Note that the reduced r^2 of the FE group is due to a substantial reduction in the range of CL over which the data were fitted. The results of performing functional regressions of $\log_e$ (weight) on $\log_e$ (CL) are also given.

During the analysis an anomalous bimodal distribution of weight at length emerged. The bimodality was not due to sexual class (M, FØ, or FE) and clearly diminished to a unimodal weight distribution as CL increased from 15 to 40 mm. We have no explanation for these data.

Reproductive Biology

The reproductive season of *H. laevigatus* was estimated by plotting the percentage of ovigerous females relative to total females against the month sampled. For the data which overlapped 1983 and 1984 no interannual difference was evident (i.e., the timing of reproduction was similar), so the data were pooled by month between these years. The results are presented in Figure 2 where the data have been further aggregated into 2-mo "seasons". For each the percentage of females bearing eggs is plotted with its 95% confidence interval and associated sample size given above.

The data show an increased incidence of ovigerous females from August to February (>30% of females). In particular over 50% of all sampled females carried eggs from October to January. Relatively few shrimp were caught with eggs during the period from April to July (<10%). Moreover,

[7]J. J. Polovina, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, NI 96822-2396, pers. commun. June 1985.

TABLE 2.—Parameter estimates of functional regressions on linear size measurements. All measurements in millimeters and all sample sizes n = 5,920.

Dependent variable	Independent variable	Slope	Intercept	Correlation coefficient
Total length	Carapace length	2.864	10.182	0.963
Carapace width	Carapace length	0.613	−5.562	0.964
Carapace length	Total length	0.349	−3.536	0.963
Carapace length	Carapace width	1.630	9.098	0.964
Carapace width	Total length	0.214	−7.737	0.902
Total length	Carapace width	4.673	36.153	0.902

TABLE 3.—Functional and predictive length-weight regressions for *Heterocarpus laevigatus*. The natural logarithm of weight in grams is fitted to the natural logarithm of carapace length in mm. The standard errors of the slope (b) and intercept (a) are given by S_b and S_a respectively.

		Slope	Intercept	S_b	S_a	n	r^2
Males	Predictive	2.755	−6.809	0.0176	0.0629	2,788	0.8976
	Functional	2.910	−7.358	—	—	—	—
Females without eggs	Predictive	2.605	−6.252	0.0185	0.0671	2,202	0.8999
	Functional	2.745	−6.757	—	—	—	—
Females with eggs	Predictive	1.815	−2.986	0.0550	0.2114	928	0.5401
	Functional	2.470	−5.498	—	—	—	—

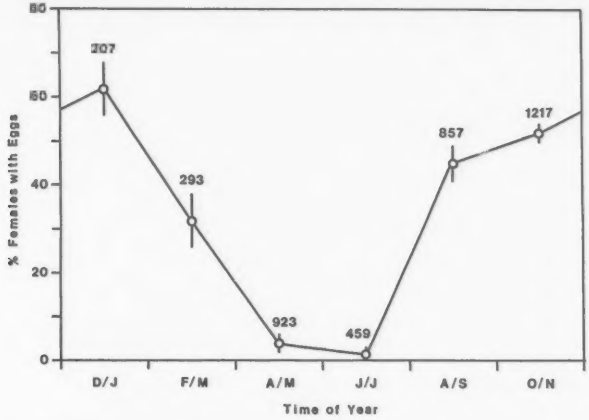


FIGURE 2.—Seasonal incidence of ovigerous *Heterocarpus laevigatus* females in the Hawaiian Islands. Vertical bars represent 95% confidence intervals and sample sizes are presented above. Site locations vary.

when the analysis was restricted to mature females only (see next section) the seasonal pattern of egg-bearing was unchanged. From these results we conclude that in Hawaiian waters *H. laevigatus* reproduces during the fall and winter seasons (August-February).

The size at maturity of female shrimp was determined by aggregating the female data into 5 mm CL classes and plotting the incidence of ovigerous females against CL class (Fig. 3). Only samples obtained during the reproductive season were included in the analysis. As before, the overall percentage

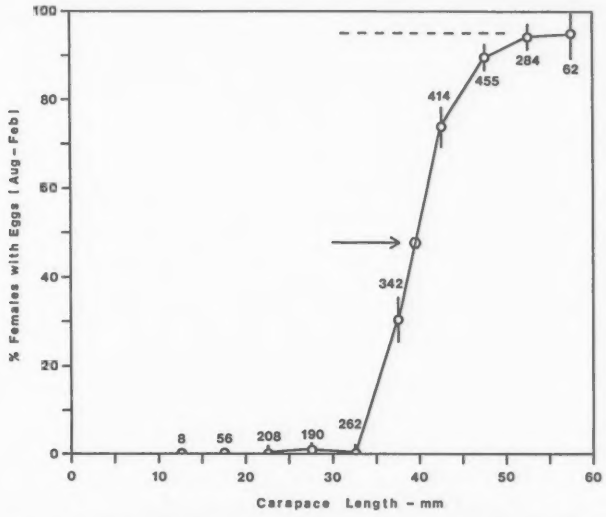


FIGURE 3.—Size at maturity for female *Heterocarpus laevigatus* sampled during the reproductive season. Vertical bars represent 95% confidence intervals and sample sizes are presented above.

with 95% confidence limits and sample sizes are provided.

The data show that the 55-60 mm CL class encompassed the largest shrimp observed. Virtually all (95%) females >50 mm CL that were sampled during August-February bore eggs. Conversely, up to 35 mm CL no more than 1% of the shrimp examined were ovigerous. The figure shows further that at a CL of 40 mm the percentage of ovigerous females is one-half its maximum value, with 48% of all sampled females bearing eggs. We conclude that females become sexually mature at this size (Gunderson et al. 1980). We have no data on maturation in males.

The data presented in Figure 4 show the sex ratio of shrimp as it depends on size (CL mm). Plotted are the percentage females, with 95% confidence intervals and sample sizes, against 5 mm CL size classes. The data clearly show that *H. laevigatus* maintains a relatively uniform sex ratio from 10 to 45 mm CL, but that females predominate in the largest length categories (45-65 mm CL).

Because some studies (Clarke 1972; Wilder 1977) have indicated that *Heterocarpus* females may experience mass mortality after egg bearing, we examined the relationship of sex ratio to season (Table 4). Presented for each 2-mo sampling period are the number of females and total number of shrimp sampled, the proportion which are female, and the standard error of the proportion. The results show that an unusually high fraction (0.72) of the shrimp sampled during the peak of the reproductive season (December-January) are female. Note that the incidence of females in trap samples declines significantly to a value of 0.45 in April-May as the breeding season wanes. At first inspection these data support the contention that females experience increased mortality after bearing eggs, i.e., that *H. laevigatus* may be semelparous.

TABLE 4.—Sex ratio of *Heterocarpus laevigatus* by month sampled. The standard error of the proportion is given by S_p.

Month	Number of females	Proportion of females	n	S_p
December-January	207	0.72	285	0.026
February-March	293	0.55	530	0.022
April-May	923	0.45	2,020	0.011
June-July	459	0.54	842	0.017
August-September	857	0.55	1,542	0.013
October-November	1,217	0.56	2,148	0.011

Spatial Distribution

The relationship between the sex ratio of *H. laevigatus* and sampling depth is provided in Table 5. These results demonstrate that the relative abundance of the two sexes is not independent of depth (χ^2 = 165.6, df = 16, $P < 0.001$). As depth increases (440-760 m) there is a significant decline in the percentage of females in our samples (P = 0.05).

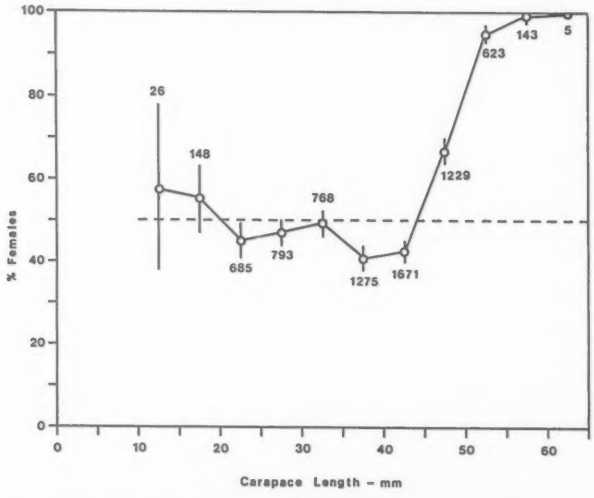


FIGURE 4.—Sex ratio as a function of carapace length. Vertical bars represent 95% confidence intervals and sample sizes are presented above.

TABLE 5.—Sex ratio and size of *Heterocarpus laevigatus* by depth (M is for males, FØ for females without eggs, and FE for females with eggs). S_p is the standard error of the proportion.

Depth (m)	Number of females	N	Proportion of females	S_p	Carapace length			
					All	M	FØ	FE
440	41	71	0.58	0.059	40	34	43	48
60	9	11	0.81	0.116	39	36	40	—
80	65	141	0.46	0.042	38	33	42	49
500	155	230	0.67	0.031	42	34	45	49
20	287	430	0.66	0.023	43	40	45	46
40	419	943	0.44	0.016	37	35	40	49
60	193	487	0.39	0.022	37	36	38	45
80	280	500	0.56	0.022	39	35	42	47
600	282	498	0.56	0.022	38	35	38	46
20	284	463	0.61	0.023	39	35	34	48
40	325	581	0.55	0.021	38	37	32	47
60	109	210	0.51	0.034	37	34	35	44
80	95	167	0.56	0.038	39	37	35	48
700	90	222	0.40	0.033	36	36	31	43
20	399	738	0.54	0.018	39	38	32	47
40	68	126	0.53	0.044	40	37	33	48
60	14	46	0.30	0.068	34	34	28	42

The results presented in Table 5 also show the distribution of mean size (CL mm) by depth (m) for all *H. laevigatus* caught, and for the M, FØ, and FE subgroups. For all shrimp combined, average size decreases slightly with increasing depth fished. The trend for decrease in size with increasing depth is not evident in the M subgroup. However, the FØ class demonstrates a strong relationship of decreasing mean CL with depth. For the FE category the decline is much less apparent, if at all. Thus the overall decline in mean CL of all shrimp combined, is clearly due to an overriding influence of females without eggs. We interpret these trends, or lack thereof, to indicate that young (i.e., small) females may move from deep to shallow water as they mature.

There is some evidence that the depth distribution of *H. laevigatus* changes with reproductive activity (i.e, season). Figure 5 presents the depth distributions for reproductively competent (>40 mm CL) male and female shrimp, classified into samples taken outside (March-July) and during the reproductive season (August-February). Note that depth distributions of both male and female shrimp are

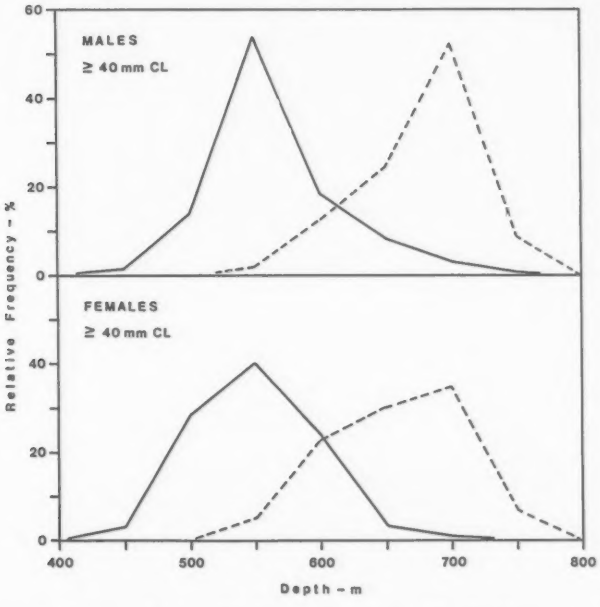


FIGURE 5.—Seasonal distributions of large (>40 mm) male and female *Heterocarpus laevigatus* by depth. The dashed line represents the spawning season distribution (May-February) and the solid line represents the distribution during the nonspawning season (March-July).

shifted 150 m deeper when the females are ovigerous. Although the data are not corrected for what may have been differences in fishing effort by depth, it is true that fishing was targeted to depths of maximum shrimp abundance. Based on these findings, and the results presented in Table 5, our data are consistent with a hypothesis of gradual movement of small females from deep to shallow water, with mature shrimp moving between depths of 550 and 700 m in synchrony with the ovigerous cycle of females.

Growth and Mortality

Clarke (1972) and King (1983) have suggested that *Heterocarpus* spp. may breed once and die. Indeed the results already presented in Table 4 may be considered consistent with the hypothesis that at least female *H. laevigatus* are semelparous. To further address this question we examined the size structure of male and female shrimp classified as follows: 1) during the latter half of the reproductive season (January-February) and 2) immediately following the reproductive season (March-July). If postreproductive mortality of shrimp was severe, a decrease in the relative abundance of large, breeding adults would be expected as the reproductive season waned.

The results presented in Figure 6 conflict with this expectation, where it is apparent that the proportional representation of large reproductive individuals (>40 mm CL) is actually greater imme-

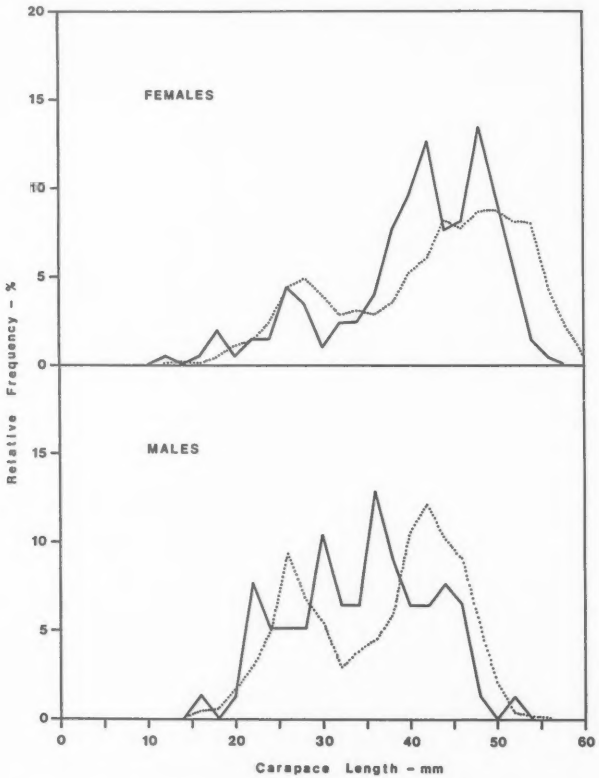


FIGURE 6.—Relative size-frequency distributions of male and female *Heterocarpus laevigatus* during the peak and postreproductive seasons. The solid line represents the peak season (January-February), males N = 78, females N = 207; the dashed line is based on data collected immediately after the peak season (March-July) males N = 1,717, females N = 1,675.

diately following than during the latter half of the reproductive season.

The total sample CL-frequency distribution of males and females combined was analyzed by the regression method of Wetherall et al. (in press) to estimate L_∞ and Z/K. When all shrimp are pooled (N = 7,368), an estimate of L_∞ = 61.7 mm CL results. Further, the ratio of total mortality rate to von Bertalanffy growth coefficient (Z/K) is estimated to be 2.6. Calculations were repeated for separate male and female subgroups, where it was found that L_∞ = 57.9 and 62.5 mm CL and Z/K = 4.3 and 2.9 for males and females, respectively. These results indicate that males generally grow to a smaller size than females.

The results of analyzing the progression of CL size modes in frequency distributions of male and female *H. laevigatus* provided preliminary estimates of K = 0.35 yr^{-1} for males and 0.25 yr^{-1} for females. The former result must be viewed with caution, however, because two "solutions" were detected by the computer search algorithm (Pauly 1982) which differed little in fit. One of these, K = 0.70 yr^{-1}, we believe to be unjustifiably high in light of the minor difference (8%) between the L_∞ of males and the L_∞ of females obtained from the regression analysis. Note that estimates of K and L_∞ typically show a strong inverse correlation (Gallucci and Quinn 1979). These results, in conjunction with the estimates of Z/K for male and female shrimp presented earlier, provide the basis for preliminary estimation of total mortality rate. We estimate Z = 1.51 yr^{-1} for males and 0.73 yr^{-1} for females, corresponding to annual survivorship fractions of 22% and 48% per year, respectively. These data indicate that males grow faster while experiencing a substantially greater total mortality rate than females.

DISCUSSION

Earlier it was assumed that, aside from depth, all shrimp samples were drawn from locations which are dynamically homogeneous; i.e., the behavior of shrimp populations through time does not vary from site to site. This is clearly a restrictive and simplifying assumption and is without doubt the major limitation on the results presented here. Nonetheless, it was a necessary simplification for us to analyze the commercial fishing data upon which this study was based. Consequently, we view those results which rely upon this assumption as tentative and in need for further validation.

Examination of the seasonal trend in the relative abundance of ovigerous females showed that in Hawaii over 50% of *H. laevigatus* females bear eggs from October to January, with a peak between August and February. Wilder (1977) found a similarly timed but more narrowly defined breeding season for *H. laevigatus* in Guam, where the percentage of ovigerous females in trap catches reached a maximum during December, but was not particularly high in any other month. Clarke (1972) reported that *H. ensifer* in Hawaii also reproduces in the winter. The breeding season of these shrimps is unusual among Hawaiian crustaceans and fishes, which typically reproduce during the spring and summer and uncommonly during the winter (Watson and Leis 1974; Lobel 1978; Uchida et al. 1980; Uchida and Tagami 1984; Walsh 1984).

Our data also indicate that in Hawaii sexual maturity of female ono shrimp occurs at approximately 40 mm CL, a size similar to that reported by King (1983) for shrimp from Fiji, Vanuatu, West Samoa, and Tonga and by Moffitt and Polovina (fn. 5) for samples from the Marianas. Based upon the estimated parameters of the von Bertalanffy growth equation derived here, this corresponds to an age of first maturity of 4 yr. Although we have no data on the maturation of males, we believe they probably mature earlier and at smaller size, perhaps at age 3 when they are 37-38 mm CL. Such a result is consistent with the findings of Moffitt and Polovina (fn. 5) who found that male *H. laevigatus* in the Marianas mature at a smaller size than do females.

Wilder (1977) speculated that both *H. ensifer* and *H. laevigatus* in Guam are protandrous hermaphrodites, as did Clarke (1972) for Hawaiian populations of *H. ensifer*. However, the results presented in King and Moffitt (1984) tend to contradict this conclusion. These authors studied the morphometry and sexuality of five deepwater pandalids, including *H. laevigatus*, in Fiji and the Marianas. Using the relative length of the appendix masculina expressed as a proportion of CL, they found no tendency toward protandrous hermaphroditism. Moreover, the sex ratio reported in their study was approximately 1:1.

Our results also indicate that for Hawaiian populations of *H. laevigatus*, and we speculate for most tropical pandalids, a sex transition does not occur. Wenner (1972) has termed the pattern exhibited in Figure 4 the standard sex ratio pattern, as distinguished from one of reversal. Due to the large numbers of females in small size classes, these data are generally inconsistent with a protandric hermaphroditic life history, as has been hypothesized by previous workers on *Heterocarpus* spp. (Clarke

1972; Wilder 1977). King and Moffitt (1984) also argue for dioecy in this species based upon relative changes in the morphology of the appendix masculina.

Evidence now exists to suggest that the sex ratio of *H. laevigatus* undergoes a seasonal change (Table 4), although the reasons for this are at present unknown. A biological alteration in population structure of this order seems unlikely. Rather, the relatively high catch of females during the December-January period may be due to seasonal changes in catchability or vulnerability of one or both sexes to the traps. Alternatively, the spatial dispersion of *H. laevigatus* may depend on sex. If males and females are spatially segregated, the high proportion of females in the December-January sample may have been due to small sample size (N = 207).

We have also shown that sex ratio depends strongly on the depth sampled (Table 5), with diminishing representation of females as depth increases. This spatial heterogeneity between the sexes may be due to directed movements. Based on size trends of females we conclude that they recruit to deeper water and subsequently migrate to shallower water. We have no evidence for similar movement of males.

Studies by King (1983) on Pacific *Heterocarpus* spp. showed cyclic migrations in these shrimps, suggesting that depth distribution may change seasonally, with an annual migration up and down the slope of the sea floor. The data presented in Figure 5 indicate that mature *H. laevigatus* in Hawaii do migrate seasonally, demonstrating distinct shifts in the depth distributions of both sexes during the reproductive season. Because this result is confounded by what may be a location effect, however, we view them as preliminary and in need of further confirmation. King (1983) also reported that *Heterocarpus* spp. were found in stomachs of tuna in Fiji, indicating perhaps some type of vertical migration in the water column.

King (1985), based on work completed in Fiji, examined the question of iteroparity and semelparity in several genera of pandalid shrimp (*Plesionika*, *Saron*, *Parapandalus*, and *Heterocarpus*). Based on the difference between length at sexual maturity and maximum length, he concluded that shallow-water species (e.g., *H. ensifer*) are semelparous. He states that deepwater *Heterocarpus* spp. "have an extended reproductive lifespan, the length of which may be taken to indicate the number of spawnings." We conclude, based on the relative size-frequency distributions of males and females during peak and postreproductive seasons, that both sexes survive well after reproducing—evidence in favor of iteroparity. Although a high mortality of shrimp following the breeding season would be evidence consistent with a semelparous life history, it is not a sufficient result to prove it. This is because each female, before dying, could have sequential multiple clutches during the October-February ovigerous period. Nonetheless, good survival of *H. laevigatus* females after carrying eggs (Fig. 6) is indicative of iteroparous reproduction.

The regression technique of Wetherall et al. (in press) produced estimates of the ratio of mortality to growth coefficient of 2.9 and 4.3 for females and males respectively. Moffitt and Polovina (fn. 5), using similar methods, estimated L_∞ = 55.2 mm CL and Z/K = 2.5 for combined male and female samples of *H. laevigatus* from essentially unfished stocks in Guam and the Marianas. Ralston (1986) also reported that the Z/K ratio of an unexploited population of *H. laevigatus* at Alamagan in the Marianas was about 2.0. The differences between estimates may therefore relate to differences in levels of exploitation. Moreover, the higher mortality rate of male shrimp when compared with females (1.51 versus 0.73 yr^{-1}) may explain the somewhat biased sex ratio in favor of females.

ACKNOWLEDGMENTS

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LITERATURE CITED

CLARKE, T. A.
1972. Exploration for deep benthic fish and crustacean resources in Hawaii. Univ. Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 29:1-18.

BMDP.
1977. BMDP Biomedical Computer Programs, P-Series. Univ. Calif. Press, Los Ang., 880 p.

DEPARTMENT OF LAND AND NATURAL RESOURCES.
1979. Hawaii fisheries development plan. Department of Land and Natural Resources, State of Hawaii, 297 p.

GALLUCCI, V. F., AND T. J. QUINN II.
1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14-25.

GOODING, R. M.
1984. Trapping surveys for the deepwater caridean shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 46(2):18-26.

GUNDERSON, D. R., P. CALLAHAN, AND B. GOINEY.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.

KING, M. G.
1983. The ecology of deepwater caridean shrimps (Crustacea: Decapoda: Caridea) near tropical Pacific Islands with particular emphasis on the relationship of life history patterns to depth. Ph.D. Thesis, Univ. South Pacific, Suva, Fiji, 258 p.

KING, M. G., AND A. J. BUTLER.
1985. Relationship of life-history patterns to depth in deepwater caridean shrimps (Crustacea: Natantia). Mar. Biol. (Berl.) 86:129-138.

KING, M. G., AND R. B. MOFFITT.
1984. The sexuality of tropical deepwater shrimps (Decapoda: Pandalidae). J. Crustacean Biol. 4:567-571.

LOBEL, P. S.
1978. Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pac. Sci. 32:193-207.

OISHI, F.
1983. Pacific Tuna Development Foundation - State of Hawaii shrimp industry development project. State Hawaii, Dep. Land Nat. Resour., Div. Aquat. Resour., 22 p.

PAULY, D.
1982. Studying single-species dynamics in a tropical multispecies context. *In* D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries. ICLARM and CSIRO, Manila, 360 p.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

STRUHSAKER, P., AND D. C. AASTED.
1974. Deepwater shrimp trapping in the Hawaiian Islands. Mar. Fish. Rev. 36(10):24-30.

UCHIDA, R. N., AND D. T. TAGAMI.
1984. Biology, distribution, population structure, and preexploitation abundance of spiny lobster, *Panulirus marginatus* (Quoy and Gaimard), in the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. T. Tanoue (editors), Proceedings of the Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 1, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii, p. 157-198. UNIHI-SEAGRANT-MR-84-01.

UCHIDA, R. N., J. H. UCHIYAMA, D. T. TAGAMI, AND P. M. SHIOTA.
1980. Biology, distribution, and estimates of apparent abundance of the spiny lobster, *Panulirus marginatus* (Quoy and Gaimard), in waters of the Northwestern Hawaiian Islands: Part II. Size distribution, legal to sublegal ratio, sex ratio, reproductive cycle, and morphometric characteristics. *In* R. W. Grigg and R. T. Pfund (editors), Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii, p. 131-142. UNIHI-SEAGRANT-MR-80-04.

WALSH, W. J., III.
1984. Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. Ph.D. Thesis, Univ. Hawaii, Honolulu, 475 p.

WATSON, W., AND J. M. LEIS.
1974. Ichthyoplankton of Kaneohe Bay, Hawaii. Univ. Hawaii Sea Grant Publ. UNIHI-SEAGRANT-TR-01, 178 p.

WENNER, A. M.
1972. Sex ratio as a function of size in marine crustacea. Am. Nat. 106-321-350.

WETHERALL, J. A., J. J. POLOVINA, AND S. RALSTON.
In press. Estimating growth and mortality in steady state fish stocks from length-frequency data. ICLARM/KISR Conf. Theory and Application of Length-Based Methods for Stock Assessment.

WILDER, M. N.
1977. Biological aspects and the fisheries potential of two deepwater shrimps, *Heterocarpus ensifer* and *H. laevigatus* in waters surrounding Guam. M.S. Thesis, Univ. Guam, Agana, Guam, 79 p.

AN INTENSIVE FISHING EXPERIMENT FOR THE CARIDEAN SHRIMP, *HETEROCARPUS LAEVIGATUS*, AT ALAMAGAN ISLAND IN THE MARIANA ARCHIPELAGO

STEPHEN RALSTON[1]

ABSTRACT

During January 1984 an intensive fishing experiment for the deepwater caridean shrimp, *Heterocarpus laevigatus*, was conducted near Alamagan Island in the Mariana Archipelago. Twenty standard shrimp traps were set daily, producing a significant decline in the average catch rate from 3.33 to 1.82 kg/trap-night over a 16-day period. This drop was associated with a removal of 776 kg of shrimp from the study site. Resampling the area 4 months later showed that the catch rate remained depressed. Length-frequency data demonstrate that the decrease in catch per unit effort was due to a decline in the number of shrimp caught. An initial population size of 1,714 kg from 312 ha habitat is estimated, corresponding to one exploitable shrimp per 51 m^2. The estimate of catchability (0.001945 trap-night^{-1}) indicates that *H. laevigatus* may be easily overfished by trapping.

Intensive fishing experiments can provide the ideal complement to resource surveys using catch per unit effort (CPUE) to estimate the relative abundance of exploitable stock. Whereas values of CPUE are usually adequate for studying spatial and temporal variation in resource abundance, often an absolute estimate of exploitable biomass is required. This is particularly true of yield assessments. Due to the relative nature of CPUE statistics, a conversion factor is necessary to translate catch rates into absolute units of biomass. This proportionality is termed catchability, typically a constant parameter (but see Schnute 1983; Polovina 1986) which can be estimated from the results of intensive fishing experiments (Ricker 1975).

The advantages of intensive fishing over alternative methods of estimating the catchability coefficient (q) are several. Foremost is that no history of either catch or effort data is needed. This characteristic makes methods of fishing success (Ricker 1975) or survey-removal (Schnute 1983) particularly attractive for use in assessments involving exploratory survey data, as well as for studying emerging new fisheries. A second advantage is that results can be obtained rapidly. Because fishing is, by definition, conducted intensively over a short time period and the necessary computations are quite simple, an estimate of q is quickly realized.

Although these advantages recommend the approach, two restrictive assumptions must be made in analyzing the data. One must assume, in the absence of information to the contrary, that the population fished is closed, or equivalently, that additions exactly balance removals other than those due to fishing. The basis of this assumption can be strengthened if the intensive fishing site is located in a naturally isolated area. For example, Polovina (1986) performed an intensive fishing experiment on a small pinnacle 5.5 km in circumference which was isolated by 75 km of deep water from the nearest similar habitat. A second assumption is that fishing removals account for all changes in stock biomass, i.e., natural mortality, growth, and recruitment are negligible during the period of fishing. For this reason, removals are carried out intensively over as short a time interval as possible. If both assumptions hold then q can be estimated directly by the slope of the linear regression of either CPUE on cumulative catch (Leslie and Davis 1939) or log{CPUE} on log{cumulative effort} (DeLury 1947).

Refinements to these two basic methods have been proposed by Braaten (1969), Crittenden (1983), Schnute (1983), and Polovina (1986) among others. Generally, estimators have been found to be most sensitive to a departure from the assumption of constant catchability. A variety of adjustments have been used to correct this and other statistical problems which often occur with real data.

The work reported here is an application of the intensive fishing method to estimate the catchabil-

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ity and population density of a deepwater caridean shrimp, *Heterocarpus laevigatus*. This circumglobal species is found in depths of 400-950 m in subtropical and tropical latitudes (King 1984). Experimental trapping surveys have shown it to be abundant at widespread localities in the central and western Pacific (King 1983), and a developing commercial fishery for this species has emerged in the Hawaiian Islands (Gooding 1984). Interest by Pacific island nations in promoting the harvest of this shrimp is great (King 1981), providing the impetus for an assessment of the *Heterocarpus* resource in the Mariana Archipelago. Additional results of this research program are reported elsewhere (Moffitt and Polovina[2]).

MATERIALS AND METHODS

Intensive fishing for *Heterocarpus laevigatus* was conducted in an area 3.5 km off the north end of Alamagan Island in the western Pacific (lat. 17°39′N, long. 145°50′E). Alamagan is part of the Commonwealth of the Northern Mariana Islands, lying 450 km north of Guam (Fig. 1). It is small, uninhabited, and of recent volcanic origin. While the ocean bottom slopes steeply away from the island at an angle of 25° to the east, south, and west, a broad shelf, approximately 6.5 km^2 in area and lying 600-800 m deep, extends well off the north end of the island. This shelf was selected as a study site because 1) good catches of *H. laevigatus* were previously obtained in the area, 2) 700 m is an ideal target depth for trapping this species (Moffitt and Polovina fn. 2), 3) the relatively uniform bottom topography would facilitate setting and retrieving fishing gear, and 4) the area had no known history of prior exploitation.

Fishing was conducted over a 16-d period, 9-24 January 1984, from the NOAA ship *Townsend Cromwell*. Shrimp traps of standard Honolulu Laboratory design were set daily in four strings of five traps each. All traps were half round in shape (91 × 66 × 46 cm), with a frame constructed of 1.27 cm reinforcing steel, covered with 1.27 × 2.54 cm mesh hardware cloth (illustrated in figure 3 of Gooding 1984). Individual traps within a set were spaced 40 m apart and were baited with three chopped Pacific mackerel, *Scomber japonicus*. All traps were set between 1100 and 1300 h in 600-800 m and were retrieved the following day between 0800 and 1100 h. In addition, a large (150 × 150 × 150 cm) pyramidal commercial shrimp trap was sometimes deployed alone.

When fishing gear was recovered, the traps were individually emptied and the contents sorted, counted, and weighed to the nearest 0.01 kg by species lot. On three occasions a random length-frequency sample of trap-caught *H. laevigatus* was saved for later study. All shrimp in these samples were measured to the nearest 0.1 mm CL (carapace length) with dial calipers.

To accurately delimit the bottom topography of the study area, an unregistered reconnaissance hydrographic survey was conducted over the site on 9 February 1984, with the *Townsend Cromwell*. Depth soundings from a Raytheon[3] fathometer were recorded every 3 min over an 8.5-h period as the vessel ran a predefined cruise track which covered the entire study area. The position of the vessel was recorded to the nearest 0.01 min at each sounding.

The *Townsend Cromwell* returned to the study site again from 12 to 16 May 1984, to assess the recovery of the *H. laevigatus* population in the study area and to determine the effect of different baiting practices on CPUE. Four sets of six traps each were set overnight on each of four occasions. Half these traps contained three chopped Pacific mackerel whereas the other half (i.e., every other one) contained two whole Pacific mackerel. The catch was sorted and treated as discussed previously.

RESULTS

Hydrographic Survey

A total of 164 depth soundings were obtained over the study site. The data were contoured using the GCONTOUR procedure of SAS/GRAPH (SAS 1981) and the resulting chart is presented in Figure 2. Solid lines represent isobath contours spaced at 200 m depth intervals. Note that the shrimp study site is a saddle point; concave upwards along the north-south axis and concave downwards from east-west. The hydrographic survey revealed a small but steep pinnacle and a deep canyon immediately adjacent to the study area.

In the figure the locations of each string of five standard traps are shown as open circles (n = 60) whereas single sets of the large pyramid trap are given as closed circles (n = 8). Fishing effort was

[2]Moffitt, R. B., and J. J. Polovina. In prep. Distribution and yield of the deepwater shrimp resource in the Marianas. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

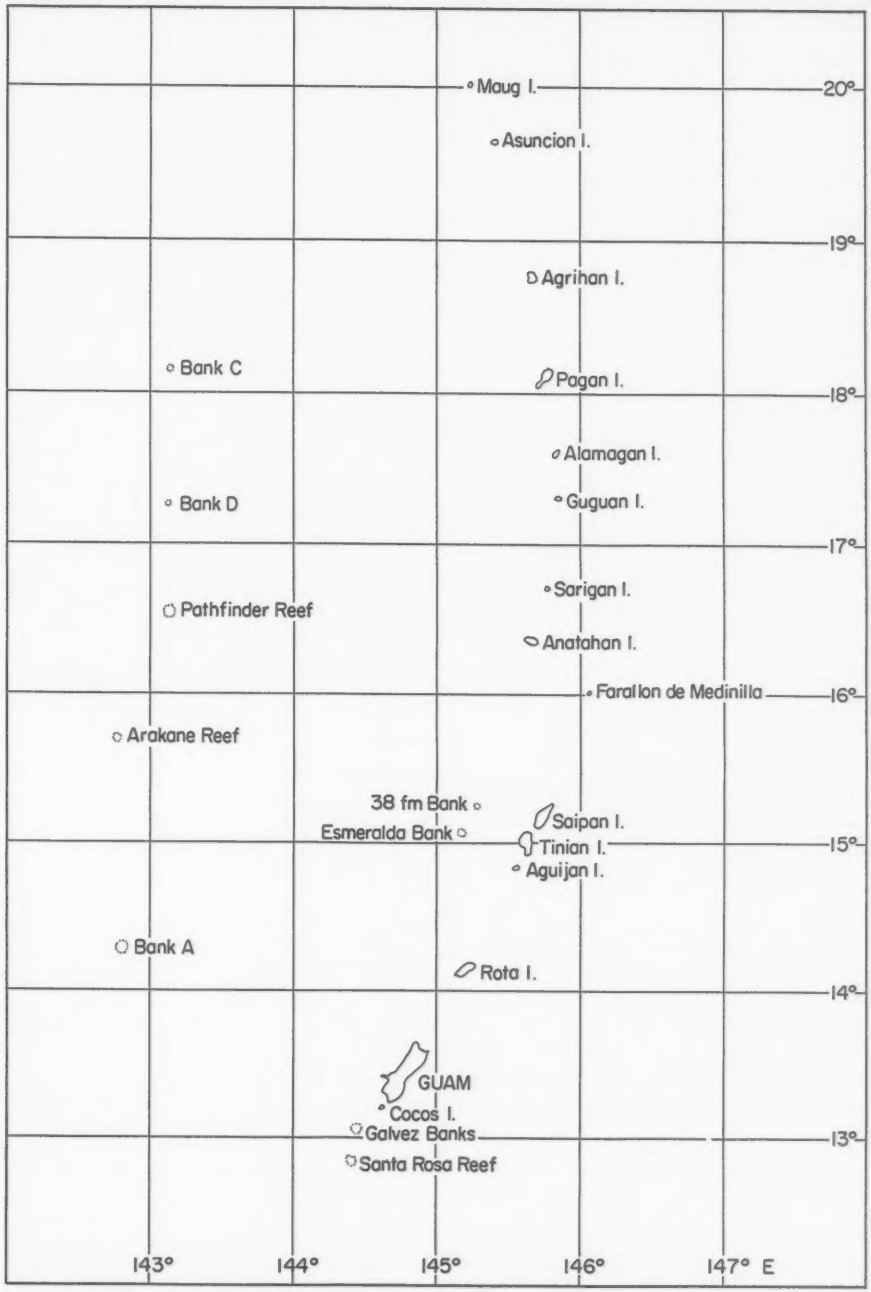

FIGURE 1.—Map of the Mariana Archipelago.

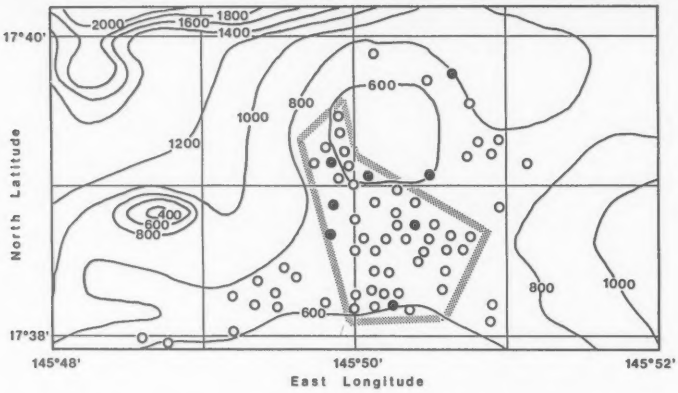

FIGURE 2.—Contour map of the Alamagan study site. Isobaths given in meters. Open circles represent set locations of standard traps (one set is composed of five traps); closed circles show sets of the pyramid trap. The stipple border encloses the area of greatest fishing intensity. One minute latitude = 1.85 km.

concentrated in the area enclosed by stipple borders, where 65% of all sets (44 of 68) occurred. This area represents 312 horizontal ha of shrimp habitat.

Intensive Fishing Experiment

Although 20 standard shrimp traps were set daily for 15 consecutive days, 29 traps were lost due to entanglement on the bottom. This resulted in 271 effective trap-nights of standard fishing effort and a gear loss rate of 9.7% (Table 1). The loss of shrimp traps is not believed to have affected the outcome of the intensive fishing experiment for two reasons: First, the Pacific mackerel bait was rapidly exhausted in the traps, as evidenced by its condition after a single night's soak; second, large holes were usually evident in traps if the fishing gear was successfully retrieved after being fouled on the bottom.

The catch of *H. laevigatus* was quite pure; only trace amounts of *H. longirostris*, *H. ensifer*, and the eel *Synaphobranchus affinis* co-occurred in the traps. The latter species was observed to consume individual *H. laevigatus* on occasion, but this had a negligible impact on overall catch rates of the shrimp.

A total catch of 663.36 kg of *H. laevigatus* was landed from standard traps, yielding an overall CPUE of 2.45 kg/trap-night (Table 1). In addition, another 112.77 kg were taken in eight sets of the pyramid trap for an overall CPUE of 14.10 kg/trap-night (Table 1). The larger commercial trap outperformed individual standard Honolulu Laboratory traps by a ratio of 5.76 to 1. Thus, one set of the large trap was roughly equivalent to one set of a string of five standard traps, but the former was much more variable in its performance. Overall, a total of 776.13 kg of *H. laevigatus* were removed from the study area during the 16-d experiment. These averaged 28 g each (16 shrimp/lb).

TABLE 1.—Summary of catch and effort statistics of the intensive fishing experiment for *Heterocarpus laevigatus* at Alamagan Island, 9-24 January 1984. All catches in kilograms and effort in standard trap-nights. CPUE includes only standard trap catches.

Date (mo/d/yr)	Standard trap catch	Pyramid trap catch	Corrected cumulative catch	Daily effort	CPUE
1/9/84	62.52	—	31	20	3.13
1/10/84	42.30	37.65	102	18	2.35
1/11/84	64.61	—	175	20	3.23
1/12/84	44.96	23.86	241	17	2.64
1/13/84	85.80	6.72	322	20	4.29
1/14/84	42.90	22.98	401	19	2.26
1/15/84	47.79	—	458	15	3.19
1/16/84	34.27	6.60	503	14	2.45
1/17/84	34.57	3.18	542	19	1.82
1/18/84	34.57	2.41	579	20	1.73
1/19/84	39.01	9.37	622	20	1.95
1/20/84	41.23	—	667	20	2.06
1/21/84	27.10	—	701	20	1.36
1/22/84	28.75	—	729	14	2.05
1/23/84	32.98	—	760	15	2.20
Total	663.36	112.77		271	

The data presented in Table 1 are arranged to be fitted by the Leslie model (Ricker 1975). The CPUE was computed each day based solely on standard trap catch and effort statistics, although cumulative

removals included catches from the large commercial trap. As in Ricker (1975), CPUE is regressed against corrected cumulative catch, defined as the cumulative catch prior to the start of an interval plus half the catch taken during the interval (see also von Geldern 1961).

Standard daily CPUE is plotted against cumulative catch removed in Figure 3. The slope of the regression is significantly less than zero (one-tailed test, $t = -2.80$, df = 13, $P = 0.01$). Estimates of slope, intercept, and mean squared error were -0.001945 trap-night^{-1}, 3.334 kg/trap-night, and 0.3754 (kg/trap-night)^2, respectively. Consequently, the catchability coefficient is estimated to be $\hat{q} = 0.001945$ trap-night^{-1} and the initial population size prior to the start of fishing to be $\hat{n} = 1{,}714$ kg. Confidence intervals for these estimates are $P(0.0004 < q < 0.0034) = 0.95$ and $P(1150 < n < 6005) = 0.95$ (Ricker 1975). Notice that the confidence interval for the estimate of initial population biomass (n) is asymmetrical about the point estimate.

Crittenden (1983) and others have warned against unequal variance in plots of CPUE against cumulative catch. To test for this possibility, the absolute values of the residuals from Figure 3 were ranked and the corrected cumulative catches were ranked. A Spearman rank correlation coefficient was then calculated, resulting in $r_s = -0.189$, $P = 0.50$. From this analysis there is no evidence of heteroscedasticity. Further, there is little to suggest curvilinearity in Figure 3. A runs test (Tate and Clelland 1957) on the signs of the residuals indicates they are randomly sequenced ($P > 0.40$). This result supports the assumption of constant catchability.

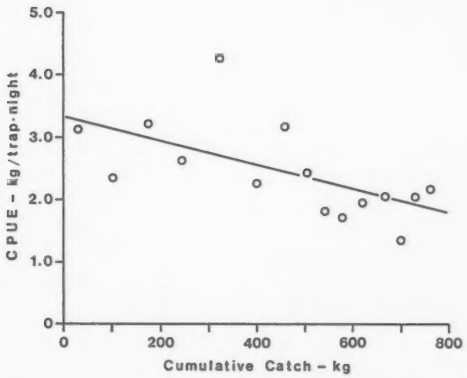

FIGURE 3.—Leslie model applied to *Heterocarpus laevigatus* at Alamagan. Each point represents 1 day of fishing. Data from Table 1.

At the time the experiment was terminated, 776 kg of shrimp had been removed by trapping. An estimate of the concomitant catch rate can be calculated from the regression equation of Figure 3. This estimate of CPUE is 1.82 kg/trap-night. When the *Townsend Cromwell* returned to the study site, 4 mo later, the mean catch rate was 1.91 kg/trap-night (42 effective standard trap-nights of effort, $s = 1.33$), this based on a total catch of 80.08 kg *H. laevigatus*. The preceding calculations include only those traps which were baited comparably to the experimental traps (three chopped Pacific mackerel). Traps with two whole baits ($n = 42$) yielded an average catch rate of 1.39 kg/trap-night ($s = 1.09$).

Length-Frequency Distributions

Examination of size-composition data can help interpret changes in weight CPUE. Declining trap catch rates could, for example, represent fewer individuals of the same size. Conversely, a decline in the average size of individuals caught with no change in numbers would also result in declining CPUE.

The three length-frequency distributions of *H. laevigatus* sampled during the period of experimental fishing are presented in Figure 4. For each distribution the date of capture, depth of capture, sample size, and mean carapace length are provided. Although appearing superficially similar, the results of ANOVA show that significant differences exist in size composition among the three samples ($F = 10.03$, df = 2, 343, $P < 0.001$). These differences, however, do not explain the decline in CPUE. The data in the figure show that the mean size of *H. laevigatus* actually increased over time, and that the overall decline in CPUE observed in Figure 2 must therefore have been due to a decrease in the number of shrimps caught.

DISCUSSION

Powell (1979) has shown that the shape of the descending limb of length-frequency distributions can provide useful information concerning the relationship between mortality and growth. Specifically, the ratio of Z (instantaneous total mortality rate) to K (von Bertalanffy growth coefficient) is defined in a simple way by the interrelationship of the least size when fully vulnerable to the gear, the mean size in the catch of fully recruited individuals, and the

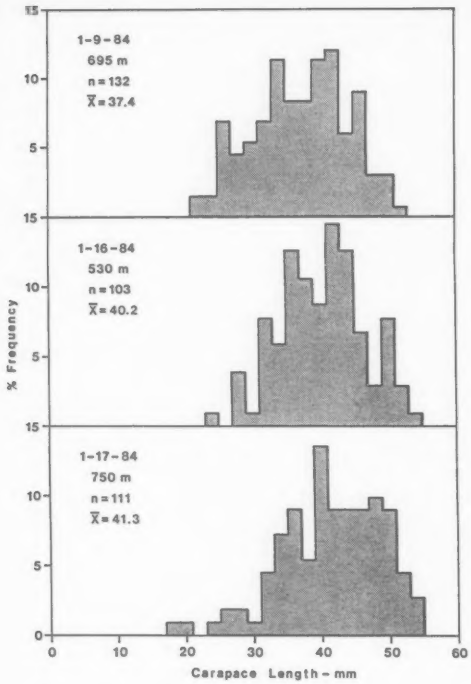

FIGURE 4.—Length-frequency distributions of *Heterocarpus laevigatus* taken in shrimp traps.

von Bertalanffy asymptotic size (L_∞). This is true if the following conditions hold: 1) the growth of individuals follows a deterministic von Bertalanffy growth curve, 2) mortality is constant and uniform for all ages, and 3) recruitment is constant and continuous over time (Beverton and Holt 1956).

Results presented in Dailey and Ralston (1986) provide the basis for estimating the minimum CL when *H. laevigatus* becomes fully recruited to the trap fishery. They provide a regression equation relating carapace width (CW) to CL. In this study the smallest mesh dimension of standard shrimp traps was 1.27 cm. This provides a logical cutoff point for measurement of least CW for shrimp that are fully vulnerable to the gear. Based on their functional regression this corresponds to 30 mm CL.

It is evident from the three panels in Figure 4 that the size distribution of *H. laevigatus* above 30 mm CL is characterized by both rising and descending portions. As shown by Powell (1979) this indicates a Z/K ratio of less than unity (i.e., instantaneous mortality rate is less than the growth coefficient). Alternatively, it is possible that the rising portions of the length distributions are not representative of the population sampled, but are instead a reflection of behavioral interactions among shrimp of different sizes. Chittleborough (1974), for example, has shown that the presence of large individuals of the decapod crustacean *Panulirus cygnus* inhibited smaller conspecifics from entering baited traps, even though smaller lobsters were vulnerable to the traps in the absence of large ones. If this kind of behavioral interaction was also in evidence here, the effective least size of *H. laevigatus* when fully vulnerable to the traps may be as large as 41 mm CL, the mode of the pooled length-frequency distribution. This would indicate a Z/K ratio of 2.0 because of the linearity of the descending portions of the size-frequency distributions. Only further experimentation will resolve this issue.

With respect to the intensive fishing experiment it is useful to consider whether or not the basic assumptions of the Leslie model were violated during the course of the study. The first of these was closure of the population. Two factors support the contention that the study population was effectively isolated and that the effects of immigration and emigration were negligible. First, the hydrographic survey showed that the study site comprised a semi-isolated extension of the main island. Continuity of prime habitat (600-800 m depth) with the island proper extended along two narrow corridors to the southeast and southwest. The shrimp has been taken as shallow as 400 m and as deep as 950 m in the Mariana Archipelago, but the 600-800 m depth range encompasses the preponderance of the region's shrimp stock (Moffitt and Polovina fn. 2), although elsewhere (e.g., Fiji, Vanuatu, and Samoa) the depth distribution apparently extends into somewhat shallower water (King 1984). The second factor arguing for closure is that the catch rate of *H. laevigatus* remained low after a 4-mo hiatus in fishing. If movements or migrations of shrimp were biologically significant over this time interval, a larger change in CPUE would be expected. It is tempting to attribute the small increase in catch rate (4.9%) to some type of biological recovery, but the estimate of mean squared error in CPUE from Figure 3 (0.3754 kg^2/trap-$night^2$) indicates that background variation is too large for the observed difference to be significant. Regardless, the data support the assumption that the population is closed.

The second assumption was that growth, natural mortality, and recruitment are negligible factors in accounting for changes in CPUE. That the experiment was completed in only 16 d and the popula-

tion was reduced an estimated 45.3% are persuasive elements here. Additionally, the size-frequency data show no indication of a major alteration in population structure. As long as the selective properties of the fishing gear remain unchanged, alterations in the length composition of the catch are not expected over short time intervals, at least due to the direct effects of fishing. Further, no recruitment of small shrimp is evident. That the mean size of *H. laevigatus* seemed to increase as the experiment progressed might support the hypothesis that growth of the stock was significant. An alternate explanation, however, is that size structure varies with depth of capture. Results from the Hawaiian Islands (Gooding 1984; Dailey and Ralston 1986) have now demonstrated this. The three samples presented in Figure 4 are confounded by this variable; other unknown factors may also have affected the shrimp size-frequency data (e.g., sexual dimorphism, contagious dispersion, sampling error, etc.). In addition, the estimated growth rate from the data (3.9 mm CL over 8 d = 0.49 mm/d) is biologically untenable.

Other investigators, notably Schnute (1983) and Crittenden (1983), have cautioned against the effects of changing catchability and unequal variance on Leslie model estimates. From the data gathered, there is little statistical evidence to suggest that these factors affected parameter estimates and I therefore assume that 0.001945 trap-night^{-1} and 1,714 kg are reasonable estimates of standard trap catchability and virgin population size, respectively.

Given that the virgin biomass of *H. laevigatus* in the study area was 1,714 kg, the next question is: How large an area was intensively fished? From Figure 2 it is clear that there is no simple answer to this question. A number of sets were located in areas peripheral to the main trapping area. Designating the stipple bordered area as the effective area fished is arbitrary, but provides a useful starting point to allow calculation of shrimp densities. This area was calculated to be 312 ha, corresponding to a projected density of 5.5 kg of exploitable *H. laevigatus* per hectare. Since individuals weighed 28 g each, on average, this is equivalent to 1 exploitable shrimp/51 m^2 of bottom, a remarkably low density. Furthermore, a catchability coefficient of 0.001945 trap-night^{-1} indicates that one unit of standard trap effort can reduce a 312-ha population of shrimp by about 0.2%. This is certainly a significant impact. The vulnerability to trapping that this species demonstrates is cause for attention and careful resource management.

ACKNOWLEDGMENTS

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LITERATURE CITED

BEVERTON, R. J. H., AND S. J. HOLT.
1956. A review of methods for estimating mortality rates in fish populations, with special reference to source of bias in catch sampling. Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer 140:67-83.

BRAATEN, D. O.
1969. Robustness of the DeLury population estimator. J. Fish. Res. Board Can. 26:339-355.

CHITTLEBOROUGH, R. G.
1974. Home range, homing, and dominance in juvenile western rock lobsters. Aust. J. Mar. Freshwater. Res. 25: 227-234.

CRITTENDEN, R. N.
1983. An evaluation of the Leslie-DeLury method and a weighted method for estimating the size of a closed population. Fish. Res. (Amst.) 2:149-158.

DAILEY, M. D., AND S. RALSTON.
1986. Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp, *Heterocarpus laevigatus*, in Hawaii. Fish. Bull., U.S. 84:915-925.

DELURY, D. B.
1947. On the estimation of biological populations. Biometrics 3:145-167.

GOODING, R. M.
1984. Trapping surveys for the deepwater caridean shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 46(2):18-26.

KING, M. G.
1981. Increasing interest in the tropical Pacific's deepwater shrimps. Aust. Fish. 40(6):33-41.
1983. The ecology of deepwater caridean shrimps (Crustacea: Decapoda: Caridea) near tropical Pacific islands with particular emphasis on the relationship of life history patterns to depth. Ph.D. Thesis, Univ. South Pacific, Suva, Fiji, 258 p.
1984. The species and depth distribution of deepwater caridean shrimps (Decapoda, Caridea) near some Southwest Pacific islands. Crustaceana 47:174-191.

LESLIE, P. H., AND D. H. S. DAVIS.
1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8:94-113.

POLOVINA, J. J.
1986. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. Fish. Bull., U.S. 84:423-428.

POWELL, D. G.
1979. Estimation of mortality and growth parameters from the length frequency of a catch. Rapp. P.-v. Réun. Cons. int. Explor. Mer 175:167-169.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

SAS INSTITUTE, INC.
1981. SAS/GRAPH user's guide. 1981 ed. SAS Inst., Inc., 126 p.

SCHNUTE, J.
1983. A new approach to estimating populations by the removal method. Can. J. Fish. Aquat. Sci. 40:2153-2169.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers Publ., Inc., Danville, IL., 171 p.

VON GELDERN, C. E., JR.
1961. Application of the DeLury method in determining the angler harvest of stocked catchable-sized trout. Trans. Am. Fish. Soc. 90:259-263.

ICHTHYOPLANKTON IN NERITIC WATERS OF THE NORTHERN GULF OF MEXICO OFF LOUISIANA: COMPOSITION, RELATIVE ABUNDANCE, AND SEASONALITY

JAMES G. DITTY[1]

ABSTRACT

Ichthyoplankton samples were collected monthly between November 1981 and October 1982 in neritic continental shelf waters off Louisiana. The survey provided the first quantitative data on the abundance and seasonal occurrence of larval fishes from open coastal waters of this area. At least 48 families of fishes were represented in samples that included 107 taxa, 54 of which were identified to species. Larval densities were lowest during the winter and highest during the summer with a mean monthly density of 208/100 m^3. Five families accounted for about 90% of total larvae: Engraulidae, Sciaenidae, Clupeidae, Carangidae, and Bothidae. The five most abundant taxa overall, in order of decreasing abundance, were anchovies (Engraulidae); Atlantic croaker, *Micropogonias undulatus*; Atlantic thread herring, *Opisthonema oglinum*; gulf menhaden, *Brevoortia patronus*; and Atlantic bumper, *Chloroscombrus chrysurus*. These taxa accounted for 82% of all larvae collected. Comparison of ichthyoplankton surveys throughout the Gulf of Mexico showed that the 10 most abundant families contributed over 90% of total larval abundance in coastal surveys but less than 70% in offshore surveys. Likewise, the five most abundant taxa contributed over 80% of total larval abundance in all but one of the coastal surveys but less than 40% in the offshore surveys. These data suggest that compared with offshore waters, there are relatively fewer dominant taxa among the ichthyoplankton in neritic waters of the Gulf of Mexico.

The northern Gulf has traditionally been one of the most productive fishery areas in North America (Gunter 1967), yet seasonality and abundance of larval fishes from open waters are poorly known. Previous studies of early life history stages in this area have mainly been focused either on select taxa (Turner 1969; Fore 1970, 1971; Christmas and Waller 1975; Fruge 1977; Ditty 1984; Cowan 1985; Shaw et al. 1985) or to surveys limited in temporal and areal coverage (Walker 1978; Ditty and Truesdale 1984). Stuck and Perry (1982) surveyed the ichthyoplankton community adjacent to Mississippi Sound, while Marley (1983) conducted an egg survey and Williams (1983) a larval fish survey of lower Mobile Bay, AL. The most comprehensive studies of the offshore larval ichthyofauna in the Gulf of Mexico and adjacent areas were those of Finucane et al. (1977) from the south Texas outer continental shelf; Houde et al. (1979) from the eastern Gulf of Mexico off Florida; Richards (1984) from the Caribbean Sea; and Powles and Stender (1976) from the South Atlantic Bight area off the east coast of the United States. The objective of this paper is to provide quantitative data on the abundance and seasonal occurrence of larval fishes from open coastal waters of the northern Gulf of Mexico off Louisiana.

MATERIALS AND METHODS

Plankton samples were collected monthly between November 1981 and October 1982 (except March 1982) in neritic continental shelf waters off Louisiana. Samples were collected at six stations in a 3.2 km^2 area located about 12.9 km south-southwest of Caminada Pass, in depths of 10-12 m (Fig. 1). Collections were made with a 60 cm paired-net, opening and closing bongo-type BNF-1 sampler[2], each net was of 0.363 mm Nitex[3] mesh. Nets were lowered to depth, opened, and towed simultaneously, in series, at discrete depths (surface, middepth, and near-bottom) for about 3 min, at a ship speed of approximately 1.5 kn; all samples were collected during the day. A General Oceanics (Model 2030) flowmeter was placed in the mouth of each net to estimate volume filtered. Samples were preserved in seawater with buffered Formalin and returned to the laboratory for sorting. Fish larvae were removed from each net and identified to the lowest

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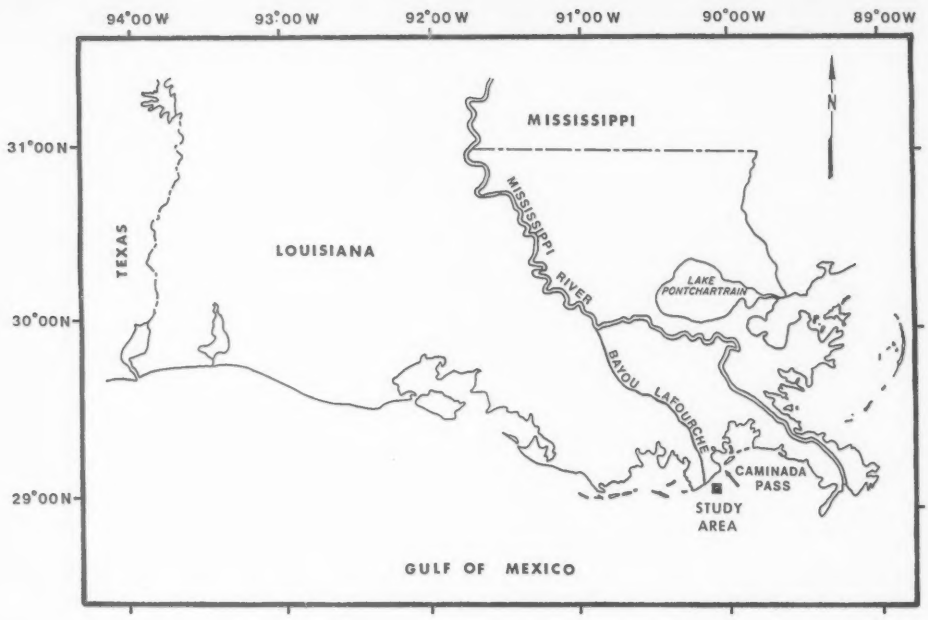

FIGURE 1.—Location of study area.

possible taxon, and standard length was measured with an ocular micrometer; all specimens were subsequently archived in 70% ethanol. Hydrographic profiles of the water column were taken at approximately 1-1.5 m intervals with a Martek Mark VI water quality monitor, except during January, February, and September 1982 when the Martek unit was inoperable. During these 3 mo, water temperatures and salinities were measured with a Beckman RS-5 inductive salinometer near surface, middepth, and bottom. Estimates of monthly mean larval densities were calculated by dividing total larvae by total volume filtered at each depth and integrated over depth. Densities are expressed as number/100 m^3. Seasonal designations were based primarily on mean surface water temperatures during the year: <20°C (Winter: December-February); 20°-25°C (Spring: April-May); >25°C (Summer: June-August); and rapidly declining surface water temperatures (Fall: September-November).

Additional data on larval occurrence and seasonality only were compiled from surface-towed meter net (0.363 mm mesh) collections at stations sampled between January 1981 and December 1982. These data consisted of four nearshore stations located adjacent to the bongo stations and were sampled monthly. Two additional groups of stations, one of four and the other of five stations, were located about 24 km south of the nearshore stations in depths of about 30 m. Each group of offshore stations was sampled quarterly but on consecutive months during 1981; thereafter, monthly samples were collected only at the four station group. These seasonality data are not discussed but are included in the Appendix Table.

Ancillary occurrence and seasonality data on larval bothids, scombrids, and sciaenids collected off Louisiana during the spring and early summer of 1982 were compiled from surface-towed 0.5 m ring net (0.505 mm mesh), 60 cm bongo net (0.333 mm mesh), and surface-towed 1 × 2 m neuston net (0.946 mm mesh) samples (SEAMAP 1983). Bongo tows were oblique and from the surface to 200 m or within 5 m of the bottom at shallower depths. Seasonality data for these taxa were compiled only from stations located between long. 88°30′W and 93°30′W and shoreward of lat. 27°00′N and, although not discussed, are also included in the Appendix Table. Additional station and cruise data are provided in Richards et al. (1984).

RESULTS

Taxonomic Problems

Larvae of many fishes in the northern Gulf of Mexico are poorly known and taxonomic problems are common, even in some of the most abundant taxa. No attempt was made to identify blennies, gobies, myctophids, synodontids, or cynoglossids to species because of the paucity of literature on larval development for these taxa. Little is also known about the taxonomy and morphological development of engraulid larvae. At least five species of engraulids are known to occur as adults in the north-central Gulf: *Anchoa mitchilli*, *A. hepsetus*, *A. lyolepis*, *A. cubana*, *Anchoviella perfasciata* (Modde and Ross 1981), and possibly *Engraulis eurystole* (Hastings 1977). *Anchoa mitchilli*, *A. hepsetus*, and *A. lyolepis* probably account for most of the engraulid larvae collected. Larvae of *A. hepsetus* and *A. mitchilli* in the Chesapeake Bay Region can be distinguished from each other primarily on placement of dorsal and anal fins (Manseuti and Hardy 1967), but this character is insufficient to separate reliably the additional species of anchovy that may occur in this area. Separation of menhaden larvae is also difficult. Three species of menhaden are known to occur as adults in this area: *Brevoortia smithi* (Chandeleur Sound, LA, eastward), *B. patronus* (Tampa Bay, FL, westward to Veracruz, Mexico) and *B. gunteri* (Mississippi Sound, MS, westward) (Christmas and Gunter 1960; Springer and Woodburn 1960; Dahlberg 1970; Turner 1971). Published descriptions are available for laboratory-reared larvae of *B. smithi* (Houde and Swanson 1975) and *B. patronus* (Hettler 1984) only. *Brevoortia gunteri* have never been described nor positively identified from the northern Gulf. Although the congeners have spawning seasons that reportedly overlap, the center of spawning of *B. patronus* is apparently off Louisiana between the Mississippi and Atchafalaya River Deltas (Turner 1969; Fore 1970; Christmas and Waller 1975). Since *Brevoortia* larvae collected during this study appear similar to that described as *B. patronus* (Hettler 1984) and because I have recognized in subsequent samples (at sizes >7 mm SL) a second morph that could be *B. gunteri*, all larvae were considered *B. patronus*.

Published descriptions of sciaenid larvae are inadequate to reliably distinguish between small larvae of the species of *Menticirrhus* (*M. americanus*, *M. littoralis*, and *M. saxatilis*) or between small *Cynoscion arenarius* and *C. nothus*. Two types of *C. arenarius* larvae were recognized primarily on the absence (Type A) or presence (Type B) of pigment in the dorsal midline immediately above the enlarged melanophore located in the ventral midline about midway along the anal fin base. Additional data on the separation of these types are provided in Cowan (1985). Small carangid larvae (<5 mm SL) of certain taxa are also difficult to identify and were referred to a morphological type when a generic or specific epithet could not be assigned. The taxonomy and/or larval development of some of the other monthly dominants (e.g., *Lepophidium* spp., *Ophidion* spp., *Auxis* spp., and *Ariomma* sp.) are poorly understood.

Hydrography

Water temperatures between November 1981 and October 1982 ranged from 16°C in January and February to 31°C in June and were below 20°C from December through February and above 25°C from May through October. There was little thermal stratification except during the summer, with stratification most pronounced in June (Fig. 2A).

Salinity stratification was most pronounced from February through August, with little stratification from September through January. Salinities were lowest near the surface, increased with depth, and ranged from <20‰ near the surface in February to 32‰ in December; salinities near the bottom ranged from 31‰ in September to 36‰ in the spring and early summer. Salinities near the surface steadily decreased from April through July and increased thereafter, whereas those near the bottom were comparatively more stable throughout the study period (Fig. 2B). In February, there was a distinct salinity gradient within the upper 6 m of the water column that ranged from 18‰ at the surface to 30‰ near middepth. In June, two distinct water masses were present with a halocline near middepth. Salinities of these two water masses differed by about 10‰ with the less saline waters above middepth (Fig. 2B). Further information on water temperature and salinity variability and the physical processes that affect the hydrography of the study area are provided in Wiseman et al. (1982).

Seasonal Composition and Abundance

At least 48 families of fishes were represented in bongo net samples that included 107 taxa, 54 of which were identified to species. About 36,500 larvae were collected, with <5% (primarily damaged or yolk-sac larvae) unidentifiable to family. The majority of larvae collected were <5 mm SL except

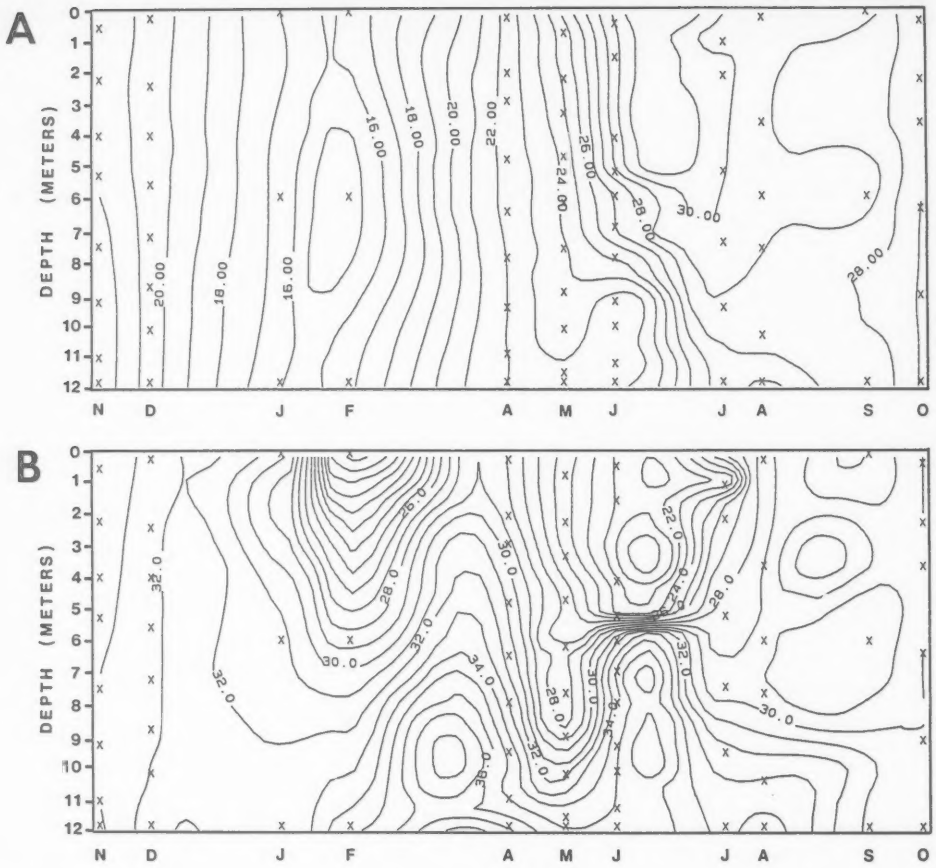

FIGURE 2.—Profiles of water temperature and salinity (November 1981-October 1982) at a representative station from the study area located in neritic waters of the northern Gulf of Mexico off Louisiana. A. Water temperature, B. Salinity. X indicates sampling depths. Collection dates were scaled by Julian calendar.

larvae of clupeiform fishes; these were usually <10 mm SL.

Generally, seasonal larval densities followed water temperatures (T) and were lowest during winter ($\bar{X}$ = 51/100 m^3 at T <20°C), increased during the spring ($\bar{X}$ = 207/100 m^3 at T <25°C), peaked during the summer ($\bar{X}$ = 394/100 m^3 at T near 30°C), and declined during the fall ($\bar{X}$ = 179/100 m^3 at rapidly declining T). Approximately 6% of all fish larvae were collected during the winter and 47.5% during the summer. Larval densities were lowest in December and highest in June, with a mean monthly density of 208/100 m^3 (Fig. 3). Overall, December had the fewest taxa (13) and September the most (37). Five families accounted for about 90% of total larvae: Engraulidae, Sciaenidae, Clupeidae, Carangidae, and Bothidae. The five most abundant taxa overall, in order of decreasing abundance, were anchovies (Engraulidae); Atlantic croaker, *Micropogonias undulatus*; Atlantic thread herring, *Opisthonema oglinum*; gulf menhaden, *Brevoortia patronus*; and Atlantic bumper, *Chloroscombrus chrysurus*. These taxa accounted for about 82% of all larvae taken. Thirty-eight taxa occurred in sufficient numbers that they were within the 10 most abundant taxa collected in at least one month. Densities of these taxa are presented in Table 1.

Anchovies accounted for about 49% of all larvae

and were collected throughout the year, but were most abundant in June and least abundant in November (Table 1). Anchovies accounted for 65% of all larvae taken during the spring and 69% during the summer, but declined to about 6% of all larvae collected during the fall and winter, respectively; anchovies were the second most abundant taxon collected during the winter and were fourth during the fall. Most anchovy larvae were collected near the surface and middepths; only 11% were collected near the bottom. A few flat anchovy, *Anchoviella perfasciata*, postlarvae were collected in February only.

Atlantic croaker accounted for 66% of all sciaenid larvae and were most abundant in November (Table 1). This species accounted for 58% of all larvae taken during the fall and for 14% of larvae overall. Most Atlantic croaker (65%) were collected near middepth with only 1% collected near the surface. Two types of sand seatrout, *Cynoscion arenarius*, were recognized with Type A collected from April to September and Type B from April to October. Of all sand seatrout larvae taken, 60% were Type A and 40% Type B, with Type A the second and Type B the third most abundant of all sciaenid larvae. Density of Type A exceeded that of Type B until September and October when Type B were more abundant (Table 1). Most Type A (66%) and Type B (56%) larvae were collected near the bottom with <5% of Type A and of Type B larvae, respectively, collected near the surface. Larvae of red drum, *Sciaenops ocellatus*, were taken during the fall only and were most abundant in September, whereas *Menticirrhus* spp. were collected in all months except December and January and were most abundant in October (Table 1). Larval densities of other less abundant sciaenids that included black drum, *Pogonias cromis*; banded drum, *Larimus fasciatus*; spot, *Leiostomus xanthurus*; silver perch, *Bairdiella chrysoura*; and silver seatrout, *Cynoscion nothus*, never exceeded 1/100 m^3. Densities of star drum, *Stellifer lanceolatus*, and spotted seatrout, *C. nebulosus*, were <2/100 m^3 for any month.

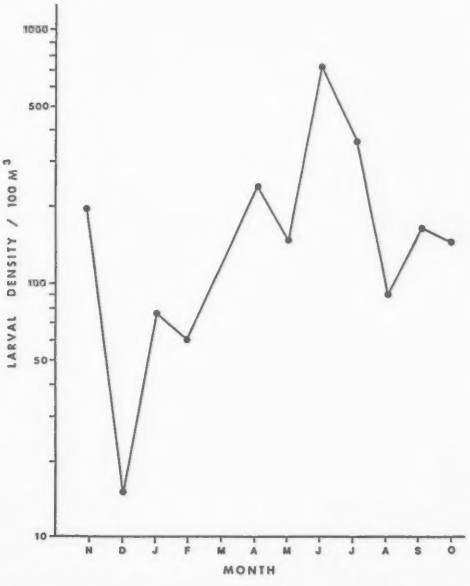

FIGURE 3.—Density of ichthyoplankton (no./100 m^3) by month, from neritic Gulf of Mexico waters off Louisiana, November 1981-October 1982.

Larvae of both the scaled sardine, *Harengula jaguana*, and Atlantic thread herring were collected from April to October, whereas gulf menhaden were collected from October to February and round herring, *Etrumeus teres*, only in January and February. No larvae of Spanish sardine, *Sardinella* sp., were identified. Densities of Atlantic thread herring were greatest in June, scaled sardine in July, and gulf menhaden in January. Densities of Atlantic thread herring accounted for about 58% of all clupeid larvae and for 9% of larvae overall; gulf menhaden accounted for 34% of all clupeids and for 5% of larvae overall. Scaled sardine accounted for 8% of all clupeid larvae. Atlantic thread herring was the second most abundant taxon collected in each season except winter, and accounted for 88% of all clupeid larvae collected between April and October; gulf menhaden accounted for 73% of all winter larvae. Over 99% of Atlantic thread herring and 80% of scaled sardine were collected when surface water temperatures were above 25°C; 90% of gulf menhaden were taken at water temperatures below 20°C. Most scaled sardine (79%) larvae were taken near the surface and only 2% near the bottom. Menhaden larvae were abundant at all depths with 37% collected near the surface and 24% near the bottom. Atlantic thread herring were most abundant near middepth (62%) and least abundant near the surface (6%).

Larvae of Atlantic bumper were collected from June to October but were most abundant in July. This species accounted for about 5% of all larvae and was the third most abundant taxon collected during both the summer and fall months. Atlantic bumper accounted for about 94% of all carangid larvae with most bumper (94%) collected when surface water temperatures averaged 30°C. Atlantic

TABLE 1.—Densities (no./100 m^3) of abundant taxa from neritic waters of the northern Gulf of Mexico off Louisiana, November 1981-October 1982[1].

Taxa	Nov.	Dec.	Jan.	Feb.	Apr.	May	June	July	Aug.	Sept.	Oct.
Engraulidae	0.8	4.0	1.6	2.9	193.8	74.3	598.1	213.4	3.0	27.6	3.3
Brevoortia patronus	7.3	2.7	67.1	41.0	—	—	—	—	—	0.8	1.4
Etrumeus teres	—	—	0.4	0.2	—	—	—	—	—	—	—
Opisthonema oglinum	—	—	—	—	0.3	52.1	71.9	2.3	16.6	62.5	(2)
Harengula jaguana	—	—	—	—	5.7	0.2	—	11.9	9.5	0.2	(2)
Synodontidae	(2)	—	(2)	0.6	—	0.3	—	—	—	—	—
Myctophidae	(2)	—	1.0	7.2	0.4	—	—	—	—	—	—
Bregmaceros cantori	0.4	(2)	—	0.1	0.3	0.5	—	—	—	—	0.1
Lepophidium spp.	0.9	—	—	—	—	—	—	—	—	—	—
Ophidion spp.	0.6	—	—	—	—	—	—	—	—	—	—
Membras martinica	—	—	—	(2)	1.0	(2)	—	—	—	—	—
Carangidae Type A	—	—	—	—	—	1.5	—	—	—	—	—
Chloroscombrus chrysurus	—	—	—	—	—	—	7.8	48.3	13.5	39.2	6.7
Oligoplites saurus	—	—	—	—	—	—	1.3	2.8	—	—	—
Trachurus lathami	—	—	—	0.4	—	—	—	—	—	—	—
Orthopristis chrysoptera	—	—	—	(2)	1.0	—	—	—	—	—	—
Archosargus probatocephalus	—	—	—	—	2.9	—	—	—	—	—	—
Lagodon rhomboides	(2)	—	0.3	0.4	—	—	—	—	—	—	—
Cynoscion arenarius (Type A)	—	—	—	—	22.5	6.3	7.2	17.2	10.3	1.9	—
Cynoscion arenarius (Type B)	—	—	—	—	10.6	0.8	6.7	11.1	10.2	5.7	1.5
Leiostomus xanthurus	0.8	0.5	0.1	0.2	—	—	—	—	—	—	—
Menticirrhus spp.	(2)	—	—	(2)	1.2	0.4	1.4	2.5	0.1	2.0	5.2
Micropogonias undulatus	182.8	2.8	—	2.2	—	—	—	—	—	—	126.4
Sciaenops ocellatus	—	—	—	—	—	—	—	—	—	12.8	6.3
Stellifer lanceolatus	—	—	—	—	1.4	0.1	1.6	0.3	0.3	0.3	0.2
Chaetodipterus faber	—	—	—	—	—	(2)	0.6	5.5	0.1	1.3	—
Mugil cephalus	—	—	0.4	(2)	—	—	—	—	—	—	—
Blennidae	0.3	1.6	0.6	(2)	2.8	9.0	1.2	2.0	0.2	0.9	0.1
Gobiidae	0.4	1.0	—	0.4	0.6	0.8	0.2	0.2	—	0.2	0.4
Auxis spp.	—	—	—	—	0.2	1.0	—	—	—	0.5	0.1
Scomberomorus maculatus	—	—	—	—	0.5	0.1	1.7	5.5	4.8	1.5	—
Ariomma sp.	—	—	0.7	—	—	—	—	—	—	—	—
Peprilus burti	1.4	0.1	0.5	0.9	0.1	0.2	0.1	—	—	—	0.5
Peprilus paru	—	—	—	—	—	0.4	0.6	0.5	0.6	4.4	(2)
Etropus crossotus	0.4	—	—	—	—	9.0	9.4	1.9	(2)	0.7	0.5
Citharichthys spilopterus	0.4	(2)	0.4	0.6	0.1	—	—	(2)	—	—	—
Symphurus spp.	0.5	0.1	—	—	0.1	1.5	2.8	1.4	0.1	0.5	0.2
Myrophis punctatus	(2)	0.1	0.1	0.2	—	—	—	—	—	—	—

[1]No data for March 1982.
[2]Density <0.1/100 m^3.

bumper were most abundant near middepth (60%) and least abundant near the bottom (9%). Other abundant carangids included leatherjacket, *Oligoplites saurus*; rough scad, *Trachurus lathami*; and carangid Type A larvae. All carangid Type A larvae were <4 mm SL and appear similar to that described as the round scad, *Decapterus punctatus*, by Aprieto (1974).

Larvae of gulf butterfish, *Peprilus burti*, occurred from October to June and harvestfish, *P. paru*, from May to October (Table 1). Most gulf butterfish (85%) larvae were collected when surface water temperatures were <25°C whereas all harvestfish were collected when surface water temperatures were above 25°C. Spanish mackerel, *Scomberomorus maculatus*, larvae occurred from April to September but were most abundant in July; most (96%) were collected when surface water temperatures exceeded 25°C. Most Spanish mackerel (74%) larvae were collected near middepth; only 5% were collected near the bottom. King mackerel, *S. cavalla*, larvae were collected only in September and at a density <0.5/100 m^3.

Many taxa occurred in relatively low abundance, and although not included in Table 1, provided additional data on seasonality. These data are presented in the Appendix Table. Only taxa with larvae <10 mm SL for a given month (except anguilliform leptocephali or sygnathids) were included in the Appendix Table, except where noted.

DISCUSSION

Data on peak seasonal occurrence of many of the abundant taxa from the present study agree with those of other coastal surveys from the north-central Gulf of Mexico off Mississippi (Stuck and Perry 1982) and off Alabama (Williams 1983). During 1982, greatest densities of larval menhaden off central Louisiana (the present study) occurred in

January-February and off western Louisiana (Shaw et al. 1985) in February-March. Stuck and Perry (1982) found larval menhaden most abundant between January and March adjacent to Mississippi Sound. These data agree with past studies (Fore 1970; Christmas and Waller 1981) from this area that reported high densities of menhaden eggs between December and February. All three of the north-central Gulf studies (Stuck and Perry 1982; Williams 1983; and the present study) reported greatest densities of Atlantic croaker during October and November; densities of sand seatrout were greatest in April, with a second smaller peak in density during either July or August. Both Atlantic bumper and Spanish mackerel were most abundant from July to September in each of these three studies. Stuck and Perry and the present study also found the greatest density of red drum in September; Williams did not sample in September. In the present study, Atlantic thread herring were most abundant in June, with a second peak in September; scaled sardine were most abundant during July and August. Few scaled sardine and Atlantic thread herring larvae were collected by Williams; no Atlantic thread herring and few scaled sardine were collected by Stuck and Perry. All three of these north-central Gulf studies also reported a bimodal peak in abundance of engraulids but differed slightly in month of peak density. Stuck and Perry, and Williams found greatest densities in April, with a second smaller peak in August. The smaller of the two peaks in abundance of engraulids occurred in April, with the greatest density in June in the present study (Table 1).

Comparison of dominant families and taxa collected overall in the present study with those of other ichthyoplankton surveys throughout the Gulf of Mexico are presented in Tables 2 and 3. Lower bay/coastal surveys were those conducted primarily inside the 10 m depth contour, except for Hoese (1965), who had a single transect of six stations out to 50 m. Offshore surveys were those conducted mainly in waters deeper than 10 m but shoreward of the edge of the continental shelf. Although not all the data listed in Tables 2 and 3 are directly comparable because of differences in gear type, mesh size, or tow, these studies provide general information on larval composition and abundance.

Most of the surveys from coastal waters (Hoese 1965; Blanchet 1979; Williams 1983; Collins and Finucane 1984; and the present study) found that engraulids dominated the summer ichthyoplankton, whereas Stuck and Perry (1982) reported engraulids second to Atlantic bumper in abundance. However, Stuck and Perry may have undersampled small engraulid and clupeid larvae because of the large mesh (1.050 mm) of their nets. Menhaden dominated the winter ichthyoplankton in all of the aforementioned coastal surveys, except Collins and Finucane (1984). These authors found that pigfish, *Orthopristis chrysoptera*, larvae were the most abundant taxa during the winter in waters off the Everglades of south Florida. All of these surveys also consistently placed engraulids and sciaenids at or near the top in total larval abundance. Overall, clupeids were relatively more abundant off south Florida (Collins and Finucane 1984) than in the other coastal surveys, except Hoese (1965), who sampled only the

TABLE 2.—Comparison of the five most abundant families collected overall from neritic waters off Louisiana with other ichthyoplankton surveys throughout the Gulf of Mexico.

Study	Engraulidae		Sciaenidae		Clupeidae		Carangidae		Bothidae		Location	Gear type, mesh size, depth of tow, and region[1]
	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%		
Present study	1	49.0	2	19.0	3	16.0	4	5.5	5	1.5	Coastal	1,6,9,10,11,15
Hoese 1965	2	42.0	3	7.0	1	45.0	—	0.5	—	0.5	Coastal	2,4,9,14
Stuck and Perry 1982	2	19.7	3	18.2	6	3.4	1	38.8	4	5.6	Coastal	3,8,9,11,15
Williams 1983	1	69.3	2	14.5	3	4.5	4	2.8	—	0.5	Lower Mobile Bay/Coastal	3,7,9,11,15
Blanchet 1979	1	75.8	2	4.9	8	1.9	7	2.2	—	<0.1	Lower Apalachicola Bay/Coastal	2,6,7,9,16
Collins and Finucane 1984[2]	2	22.5	4	6.9	1	24.1	5	6.1	—	<0.1	Coastal	2,7,9,12,18
Finucane et al. 1979[3]	5	6.2	—	<0.1	3	8.1	8	3.7	6	6.1	Offshore	1,7,13,14
Houde et al. 1979	12	2.0	30	0.3	1	20.5	6	3.9	3	6.4	Offshore	1,2,7,12,17

[1] 1 60 cm bongo; 2 1 m; 3 1 × 0.5 m rectangular; 4 0.086 mm; 5 0.333 mm; 6 0.363 mm; 7 0.505 mm; 8 1.050 mm; 9 surface; 10 middepth; 11 bottom; 12 oblique; 13 double-oblique; 14 west-central; 15 north-central; 16 north-east; 17 east-central; 18 south-east

[2] inshore data only

[3] 1977 bongo net data only

TABLE 3.—Comparison of five most abundant taxa from neritic waters off Louisiana with ichthyoplankton surveys throughout the Gulf of Mexico.

Taxa	Present study %	Hoese 1965 %	Stuck and Perry 1982 %	Williams 1983 %	Blanchet 1979 %	Collins and Finucane 1984[1] %	Finucane et al. 1979[2] %	Houde et al. 1979 %
Engraulidae	49.0		19.7	69.0	75.8	22.5	7.1	
Micropogonias undulatus	14.0			5.8				
Opisthonema oglinum	9.0					4.5		7.9
Brevoortia patronus	5.0	15.6		4.3				
Chloroscombrus chrysurus	5.0		38.4	2.8	1.8	4.8		
Harengula jaguana		29.1						
Anchoa hepsetus		24.0						
Anchoa mitchilli		17.7						
Menticirrhus spp.		2.6						
Cynoscion arenarius			12.0	8.2				
Citharichthys-Etropus complex			5.6					
Symphurus spp.			3.8					
Atherinidae					3.9			
Gobiesox strumosus					3.2			
Gobiosoma spp.					2.7			
Microgobius spp.						9.1		
Orthopristis chrysoptera						4.8		
Gobiidae							15.8	15.1
Bregmaceros atlanticus							7.1	
Saurida spp.							6.1	
Syacium spp.							4.1	
Sardinella anchovia								8.6
Decapterus punctatus								3.1
Diplectrum formosum								2.8

[1]Inshore data only.
[2]1977 bongo net data only.

surface waters of his offshore transect (Table 2).

Offshore, Houde et al. (1979) found that clupeids (Spanish sardine and Atlantic thread herring), gobiids, and bothids (mostly dusky flounder, *Syacium papillosum*) dominated summer ichthyoplankton in the eastern Gulf of Mexico off Florida, whereas clupeids (round herring and Spanish sardine), bothids (mostly gray flounder, *Etropus rimosus*), and bregmacerotids dominated the winter. In the western Gulf of Mexico off the south Texas coast, Finucane et al. (1979) reported that, during 1977, clupeids (mostly scaled sardine) and bothids (mostly *Syacium* spp.) dominated the summer and bregmacerotids and clupeids (menhaden) the winter ichthyoplankton. In the northern Gulf of Mexico off Louisiana, Ditty and Truesdale (1984) found that engraulids and carangids (mostly Atlantic bumper) dominated the summer (July 1976), whereas larvae of clupeids (mostly gulf menhaden) and gobiids dominated the winter (January-February 1976). The most abundant families collected overall off Florida were clupeids and gobiids (35.6% of all larvae), and off south Texas were gobiids and synodontids (26.7% of all larvae). The kinds of larvae (gobiids, bothids, clupeids, and bregmacerotids) that dominated these two offshore surveys were similar, but with clupeids and bothids relatively more abundant off Florida than Texas; engraulids were relatively more abundant off south Texas than off Florida (Table 2). Ditty and Truesdale (1984) found clupeids and engraulids most abundant overall (67.7% of all larvae), but their surveys were too limited temporally and in areal coverage for adequate comparison to the other two offshore surveys.

The 10 most abundant families accounted for 66.6% of all larvae collected off Florida (Houde et al. 1979) and for 68.6% off south Texas (Finucane et al. 1979). In contrast, the top 10 families in each of the coastal surveys contributed over 90% of all larvae collected. Likewise, the five most abundant taxa contributed over 80% of all larvae collected in all but one (Collins and Finucane 1984) of the coastal surveys but <40% in the two offshore surveys (Table 3).

In conclusion, there was general agreement among all three coastal surveys from the north-central Gulf of Mexico on peak seasonal occurrence of many of the abundant taxa and on the dominant families in overall larval abundance. Comparison of other coastal and offshore ichthyoplankton surveys throughout the Gulf of Mexico with the present study suggests that, when compared with offshore waters, there are relatively fewer dominant taxa

among the ichthyoplankton in neritic waters of the Gulf of Mexico.

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LITERATURE CITED

APRIETO, V. L.
1974. Early development of five carangid fishes of the Gulf of Mexico and the South Atlantic coast of the United States. Fish. Bull., U.S. 72:415-443.

BLANCHET, R. H.
1979. The distribution and abundance of ichthyoplankton in the Apalachicola Bay, Florida area. Master's Thesis, Florida State Univ., Tallahassee, 143 p.

CHRISTMAS, J. Y., AND G. GUNTER.
1960. Distribution of menhaden, genus *Brevoortia*, in the Gulf of Mexico. Gulf Coast Research Laboratory, Ocean Springs, MS, 20 p.

COLLINS, L. A., AND J. H. FINUCANE.
1984. Ichthyoplankton survey of the estuarine and inshore waters of the Florida Everglades, May 1971 to February 1972. U.S. Dep. Commer., NOAA Tech. Rep., NMFS 6, 75 p.

COWAN, J. H., JR.
1985. The distribution, transport and age structure of drums (Family Sciaenidae) spawned in the winter and early spring in the continental shelf waters off western Louisiana. Ph.D. Thesis, Louisiana State Univ., Baton Rouge, 182 p.

DAHLBERG, M. D.
1970. Atlantic and Gulf menhadens, genus *Brevoortia* (Pisces: Clupeidae). Bull. Fla. State Mus. Biol. Sci. 15:91-162.

DITTY, J. G.
1984. Seasonality of sciaenids in the northern Gulf of Mexico. Assoc. Southeastern Biol. Bull. 31(2):55.

DITTY, J. G., AND F. M. TRUESDALE.
1984. Ichthyoplankton surveys of nearshore Gulf waters off Louisiana: January - February and July, 1976. Assoc. Southeastern Biol. Bull. 31(2):55-56.

FINUCANE, J. H., L. A. COLLINS, L. E. BARGER, AND J. B. MCEACHRAN.
1979. Ichthyoplankton/mackeral eggs and larvae. NOAA Final Report to BLM. Environmental Studies of the South Texas Outer Continental Shelf 1977. BLM Contract AA550-1A7-21, 504 p.

FORE, P. L.
1970. Oceanic distribution of eggs and larvae of the Gulf menhaden. *In* Report of the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., for the fiscal year ending June 30, 1968, p. 11-13. U.S. Fish Wildl. Serv. Cir. 341.
1971. The distribution of the eggs and larvae of the round herring, *Etrumeus teres*, in the northern Gulf of Mexico. Assoc. Southeastern Biol. Bull. 18(1):34.

FRUGE, D. J.
1977. Larval development and distribution of *Micropogonias undulatus* and *Leiostomus xanthurus* and larval distribution of *Mugil cephalus* and *Bregmaceros atlanticus* of the southeastern Louisiana coast. Master's Thesis, Louisiana State Univ., Baton Rouge, 75 p.

GUNTER, G.
1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. *In* G. Lauff (editor), Estuaries, p. 621-638. Am. Assoc. Adv. Sci. Spec. Publ. No. 83.

HASTINGS, R. W.
1977. Notes on the occurrence of the silver anchovy, *Engraulis eurystole*, in the northern Gulf of Mexico. Northeast Gulf Sci. 1(2):116-118.

HETTLER, W. F.
1984. Descriptions of eggs, larvae, and early juveniles of Gulf menhaden, *Brevoortia patronus*, and comparisons with Atlantic menhaden, *B. tyrannus*, and yellowfin, *B. smithi*. Fish. Bull., U.S. 82:85-95.

HOESE, H. D.
1965. Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. Thesis, Univ. Texas, Austin, 144 p.

HOUDE, E. D., J. C. LEAK, C. E. DOWD, S. A. BERKELEY, AND W. J. RICHARDS.
1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Report to BLM, Contract No. AA550-CT7-28, 546 p.

HOUDE, E. D., AND L. J. SWANSON, JR.
1975. Description of eggs and larvae of yellowfin menhaden, *Brevoortia smithi*. Fish. Bull., U.S. 73:660-673.

MANSEUTI, A. J., AND J. D. HARDY, JR.
1967. Development of fishes of the Chesapeake Bay region: an atlas of egg, larval, and juvenile stages. Nat. Resourc. Inst., Univ. Maryland, Baltimore, 202 p.

MARLEY, R. D.
1983. Spatial distribution patterns of planktonic fish eggs in lower Mobile Bay, Alabama. Trans. Am. Fish. Soc. 112: 257-266.

MODDE, T., AND S. T. ROSS.
1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. Fish. Bull., U.S. 78:911-922.

POWLES, H., AND B. W. STENDER.
1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. South Carolina Mar. Resour. Cent., Tech. Rep. Ser. No. 11, 47 p.

RICHARDS, W. J.
1984. Kinds and abundances of fish larvae in the Caribbean Sea and adjacent areas. U.S. Dep. Commer., NOAA Tech. Rep., NMFS SSRF-776, 54 p.

RICHARDS, W. J., T. POTTHOFF, S. KELLEY, M. F. MCGOWAN, L. EJSYMONT, J. H. POWER, AND R. M. OLVERA L.
1984. SEAMAP 1982 - Ichthyoplankton: Larval distribution and abundance of Engraulidae, Carangidae, Clupeidae, Lutjanidae, Serranidae, Coryphaenidae, Istiophoridae, Xiphiidae, and Scombridae in the Gulf of Mexico. U.S. Dep. Commer., NOAA Tech. Mem., NMFS-SEFC-144.

SEAMAP.
1983. (plankton). ASCII characters. Data for 1982. [Fisheries-independent survey data]/National Marine Fisheries Service; Southeast Fisheries Center: Gulf States Marine Fisheries Commission [producer].

SHAW, R. F., J. H. COWAN, JR., AND T. L. TILLMAN.
1985. Distribution and density of *Brevoortia patronus* (Gulf menhaden) eggs and larvae in the continental shelf waters of western Louisiana. Bull. Mar. Sci. 36:96-103.

SPRINGER, V. G., AND K. D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 1, 104 p.

STUCK, K. C., AND H. M. PERRY.
1982. Ichthyoplankton community structure in Mississippi coastal waters. *In* Fishery Monitoring and Assessment Completion Report, 1 January 1977 to 31 December 1981, p. VI-I-1 thru VI-I-53. Proj. No. 2-296-R, Gulf Coast Research Laboratory, Ocean Springs, MS.

TURNER, W. R.
1969. Life history of menhadens in the eastern Gulf of Mexico. Trans. Am. Fish. Soc. 98:216-224.
1971. Occurrence of *Brevoortia gunteri* in Mississippi Sound. Q. J. Fla. Acad. Sci. 33:273-274.

WALKER, H. J., JR.
1978. Ichthyoplankton survey of nearshore Gulf waters between Barataria Bay and Timbalier Bay, Louisiana, during July, August, and December, 1973. Master's Thesis, Louisiana State Univ., Baton Rouge, 59 p.

WILLIAMS, L. W.
1983. Larval fish assemblages of lower Mobile Bay. Master's Thesis, Univ. Southern Alabama, Mobile, 55 p.

WISEMAN, W. J., JR., S. P. MURRAY, J. M. BANE, AND M. W. TUBMAN.
1982. Temperature and salinity variability within the Louisiana Bight. Contrib. Mar. Sci. 25:109-120.

APPENDIX TABLE.—Seasonality of larval fishes in the northern Gulf of Mexico off Louisiana, January 1981-December 1982.

Taxa	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Neoconger mucronatus										----		
Muraenidae				----------								
Gymnothorax sp.				----------								
Hoplunnis sp.	----------											
Congridae							----					
Ophichthidae				----					----		----	
Bascanichthys bascanium								----------				
Myrophis punctatus	----------										----------	
Ophichthus gomesii							----		----			
Pseudomyrophis 'D'											----	
Brevoortia patronus	----------								----------			----------
Etrumeus teres	----------											
Harengula jaguana				----------						----------		
Opisthonema oglinum				----------						----------		
Sardinella sp.										----		
Engraulidae	----------											----------
Anchoviella perfasciata[1]	----------								----			----
Gonostomatidae		----------										----
Cyclothone sp.	----------										----	
Vinciguerria nimbaria	----------			----								
Synodontidae	----------						----				----	
Paralepidae		----			----							
Lestidiops affinis		----										
Myctophidae	----------									----------		
Centrobranchus nigriocellatus												----
Diaphus sp.											----	
Diogenichthys atlanticus		----										
Hygophum sp.		----										
Lampanyctus sp.		----										
Gobiesox strumosus		----------										
Ceratiodei					----							----
Antennariidae				----						----		
Gigantactinidae					----							
Bregmaceros cantori	----------								----------			
Bregmaceros atlanticus										----------		
Urophycis spp.	----------										----------	
Ophidiidae					----				----		----------	
Brotula barbata	----											
Lepophidium spp.										----------		
Ophidion spp.				----						----------		
Ophidion welshi/grayi			----							----		
Ophidion selenops			----							----		
Exocoetidae						----			----			----
Hyporhamphus unifasciatus									----			
Atherinidae		----			----				----			
Membras martinica				----------								
Holocentrus sp.					----							
Macrorhamphosus scolopax	----											
Syngnathus spp.		----		----------					----			
Serranidae	----------									----------		
Anthinae	----										----	
Hemanthias leptus	----											
Grammistinae											----	
Rypticus maculatus							----					
Serraninae		----------			----					----		
Serraniculus pumilio										----		
Pomatomus saltatrix				----						----------		
Carangidae Type A[2]					----			----------			----	
Carangidae Type B[2]			----				----			----		
Carangidae Type C[2]				----------						----------		
Carangidae Type D[2]			----				----------					
Chloroscombrus chrysurus					----------					----------		
Oligoplites saurus					----------							
Selene sp.							----------			----------		
Trachurus lathami	----------											
Coryphaena equiselis					----				----			
Lutjanus sp.							----------			----------		
Gerreidae						----			----------			
Orthopristis chrysoptera		----		----								
Archosargus probatocephalus		----------										

APPENDIX TABLE.—*Continued.*

Taxa	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Lagodon rhomboides	----------										----------	
Bairdiella chrysoura				----------	----------	----------	----------	----------	----------			
Cynoscion arenarius Type A				----------	----------	----------	----------	----------	----------			
C. arenarius Type B				----------	----------	----------	----------	----------	----------	----------		
C. nebulosus				----------	----------	----------	----------	----------	----------			
C. nothus						----------			----------	----------		
Larimus fasciatus									----------	----------		
Leiostomus xanthurus	----------									----------	----------	----------
Menticirrhus spp.		----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	
Micropogonias undulatus	----------								----------	----------	----------	----------
Pogonias cromis	----------	----------	----------	----------								----
Sciaenops ocellatus								----------	----------	----------		
Stellifer lanceolatus				----------	----------	----------	----------	----------	----------	----------		
Mullidae	----			----			----					
Chaetodipterus faber					----------	----------	----------	----------	----------			
Labridae				----------	----------					----------	----------	
Scaridae												----
Mugil cephalus	----------	----------	----------								----------	----------
Mugil curema					----------			----				
Sphyraena spp.					----------	----------	----------	----------	----------	----------		
Blennidae	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
Callionymus pauciradiatus									----------	----------		
Gobiidae	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
Gobionellus hastatus	----								----------			
Microdesmus spp.				----------			----------			----		
Diplospinus multistriatus		----										
Trichiurus lepturus				----------					----------	----------		
Auxis sp.				----------	----------			----------	----------	----------		
Euthynnus alletteratus					----------	----------	----------	----------	----------			
E. pelamis				----------	----------				----			
Scomber japonicus										----------		
Scomberomorus cavalla						----------	----------	----------	----------			
S. maculatus				----------	----------	----------	----------	----------	----------			
Thunnus albacares				----					----			
T. atlanticus				----------	----------				----			
T. thynnus				----------	----------				----			
Ariomma sp.	----		----------	----------								
Cubiceps pauciradiatus				----------	----------				----------			
Nomeus gronovii	----											
Peprilus burti	----------	----------	----------	----------	----------	----------				----------	----------	----------
P. paru					----------	----------	----------	----------	----------	----------		
Scorpaena spp.					----------						----	
Prionotus spp.					----		----			----------		
Dactylopterus volitans					----							
Bothus sp.				----------								
Citharichthys sp.	----------	----------	----------	----------	----------	----------				----------	----------	----------
Citharichthys sp. Type A					----							
Citharichthys sp. Type B					----------	----------	----------					
Citharichthys sp. Type C						----						
C. cornutus				----------	----------	----------						
C. gymnorhinus												----
C. spilopterus	----------	----------	----------								----------	----------
Cyclopsetta sp.					----------	----------	----------					
Engyophrys senta					----------	----------	----------					
Etropus crossotus				----------	----------	----------	----------	----------	----------	----------		
Monolene sessilicauda					----							
Paralichthys sp.	----										----	
Syacium sp.					----------	----------	----------	----------		----------		
S. gunteri						----------	----------		----			
S. papillosum						----------	----------					
Trichopsetta ventralis					----------	----------	----------	----------				
Achirus lineatus					----------	----------	----------	----------				
Trinectes maculatus							----					
Symphurus spp.			----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
Monacanthus setifer											----	
Sphoeroides spp.				----------	----------	----------			----------	----------		

[1]Juveniles.
[2]Morph Type A may represent *Decapterus*/*Elagatis*; Type B - *Selar crumenopthalamus*; Type C - *Seriola* spp.; Type D - *Caranx* spp.

STOMACH CONTENTS AND FOOD CONSUMPTION ESTIMATES OF PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*[1]

ERIC A. REXSTAD[2] AND ELLEN K. PIKITCH[3]

ABSTRACT

Analysis of 466 stomachs of Pacific hake, *Merluccius productus*, collected during August 1983 off the coasts of Washington and Oregon indicates euphausiids comprise the most important food resource in terms of percent by weight, numbers, and frequency of occurrence for the species at that time of year. The importance of fish in the Pacific hake diet increases with the size of the hake, constituting 87% of the diet by weight in the largest individuals. Weak evidence of a nocturnal feeding pattern was observed. This indistinct nocturnal feeding pattern could have been caused by poor food availability due to El Niño. Estimates of food consumption by Pacific hake indicate that this species may have a substantial impact on some commercially valuable species such as pink shrimp, *Pandalus jordani*, even though pink shrimp is a fairly minor component of the diet. A statistically significant negative relationship between Pacific hake catch-per-unit-effort (CPUE) and pink shrimp CPUE off the west coast of the United States, using a lag of 2 years, was found.

Pacific hake, *Merluccius productus*, constitute an important component of the California Current ecosystem off the west coast of North America. It is estimated that a standing stock of approximately 1.5 million metric tons (t) exists off the Pacific coast between central California and Vancouver Island (Bailey et al. 1982). This biomass represents a substantial prey base for a variety of fish in the ecosystem: great white sharks, *Carcharodon carcharias*; soupfin sharks, *Galeorhinus zyopterus*; Pacific electric ray, *Torpedo californica*; bonito, *Sarda chiliensis*; albacore, *Thunnus alalunga*; bluefin tuna, *Thunnus thynnus*; rockfishes, *Sebastes* spp.; sablefish, *Anoplopoma fimbria*; lingcod, *Ophiodon elongatus*; dogfish, *Squalus acanthias*; and arrowtooth flounder, *Atheresthes stomias* (Bailey et al. 1982). Pacific hake also constitute a major prey item for a number of marine mammals, including the California sea lion, *Zalophus californianus*; northern sea lion, *Eumetopias jubatus*; northern fur seal, *Callorhinus ursinus*; saddleback dolphin, *Delphinus delphis*; Pacific whiteside dolphin, *Lagenorhynchus obliquidens*; and northern right whale dolphin, *Lissodelphis borealis* (Fiscus 1979).

Pacific hake also have an important impact on species below them in the food chain. Best (1963) described Pacific hake as opportunistic feeders. Their diet includes numerous species of crustacea, particularly euphausiids, several genera of shrimp, crab megalopae, and a variety of fish including Pacific herring, *Clupea harengus pallasi*; rockfish; sablefish; and flatfish (Livingston 1983). Pacific hake may compete for food resources with a host of other species that feed on the abundant euphausiid resource (Tyler and Pearcy 1975; Karpov and Cailliet 1978; Brodeur and Pearcy 1984), including commercially prized salmonids (Peterson et al. 1982).

At the top of the trophic structure is the commercial fishing fleet, comprised mainly of foreign joint-venture fishing boats that have harvested, on average, 127,000 t of Pacific hake per year since 1966 (R. C. Francis[4]).

Pacific hake migrate seasonally along the west coast of North America (Swartzman et al. 1983) and spawn in winter in the warm waters off southern California and the Baja peninsula. During the spring and summer, the adults migrate as far north as Vancouver Island to feed. The Pacific hake tend to stratify along the coast by size, with the largest individuals traveling farthest from the spawning areas and smaller juveniles remaining off the coast of California. In autumn, the adults return to the southern spawning areas (Bailey et al. 1982).

[1]Technical paper No. 7718, Oregon Agricultural Experimental Station.

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[4]R. C. Francis, Fisheries Research Institute, University of Washington, Seattle, WA 98195, pers. commun. May 1985.

The pink shrimp, *Pandalus jordani*, fishery off Oregon was one of the most economically viable fisheries during the late 1970s with landings in excess of 26,000 t in 1978. Subsequent to that time, pink shrimp landings have declined, with slightly over 2,000 t being landed in 1984 (Saelens and Zirges 1985). The purpose of this study was to describe the dietary habits of the Pacific hake and, in particular, to determine whether predation by Pacific hake on pink shrimp could explain some of the fluctuations seen in pink shrimp landings.

MATERIALS AND METHODS

In August and September 1983, during the National Marine Fisheries Service (NMFS) West Coast Groundfish Survey, Pacific hake stomachs were sampled from 41 hauls taken during daylight hours between Coos Bay, OR, and Grays Harbor, WA (Fig. 1). Tows were of 0.5-h duration using a Nor'eastern[5] high-opening bottom trawl equipped with roller gear which has an approximate horizontal opening of 13.4 m and vertical opening of 8.8 m. Further details of the sampling regime can be found in Gunderson and Sample (1980) and Weinberg et al. (1984). Between 5 and 15 individuals of each sex from a 5 cm size class (30-34 cm, 35-39 cm, 40-44 cm, 45-49 cm, 50-54 cm, 55+ cm) were sampled from each haul where practical. A total of 466 stomachs were extracted at sea and placed in cheesecloth bags. Stomachs with evidence of regurgitated contents were not included in the sample. Stomachs were preserved in a 10:1 solution of seawater to Formalin.

Stomach Content Analysis

In the laboratory, stomachs were transferred to ethyl alcohol and examined under a dissecting microscope. Stomach fullness and degree of digestion were visually estimated and given a qualitative rating (0-4 from empty to distended, and from unrecognizable to recently consumed). Contents were identified to the lowest taxon and enumerated. Wet weight of each taxon was also determined.

Diet composition was characterized by percent of total number of food items (%N), percent of total diet by weight (%W), and frequency of occurrence in nonempty stomachs (FO). An index of relative importance (IRI) was then derived from these values IRI = FO (%N + %W) (Pinkas et al. 1971).

The data were further stratified by sex, time of

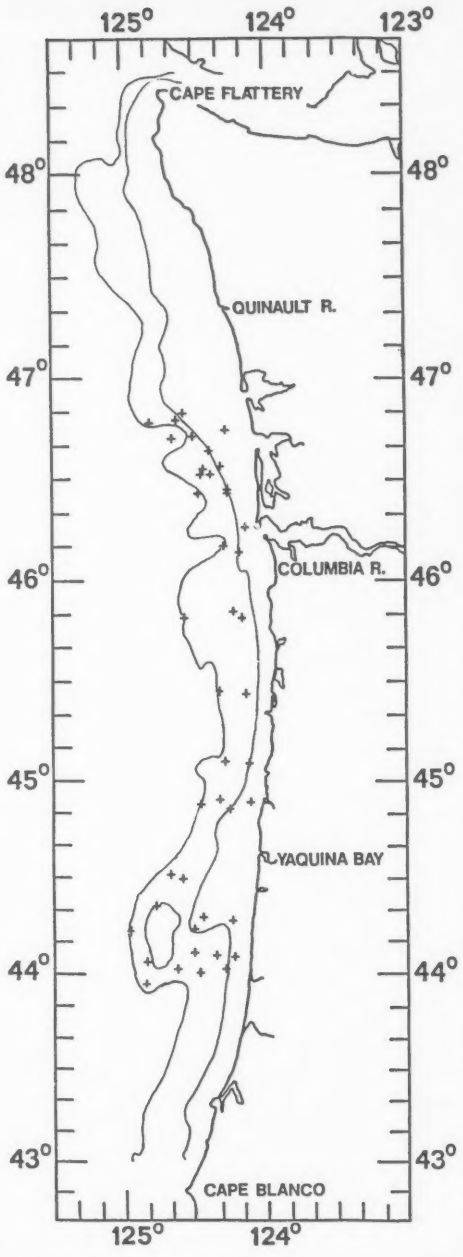

FIGURE 1.—Stations where Pacific hake stomachs were taken during 1983 NMFS West Coast Groundfish Survey; 100 and 200 m isobaths are also shown.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

collection (morning, afternoon, and evening), depth of capture (0-100 m, 100-200 m, >200 m), and size. Chi-square tests of homogeneity (Ostle and Mensing 1975) were performed on the frequency of occurrence data for each prey species in these categories.

Consumption Estimates

Using the size-specific prey consumption information derived from this study, Pacific hake population abundance estimates from the 1983 NMFS survey (Weinberg et al. 1984; Francis fn. 4) and bioenergetics estimates from Francis (1983), trophic calculations were performed to estimate ecosystem-level impacts of prey consumption by Pacific hake in the Columbia INPFC (International North Pacific Fisheries Commission) statistical area in 1983.

Biomass estimates were derived from two distinct surveys. The bottom trawl survey estimated the benthic component of the population. Details of these estimates can be found in Weinberg et al. (1984). The pelagic component of the population was estimated by hydroacoustic methods. Size composition of the pelagic segment of the population was estimated from companion midwater trawls conducted from the hydroacoustic vessel. Biomass estimates for each of the five size classes sampled were determined from estimated numbers in each centimeter size interval and length-weight regressions (Francis fn. 4).

Using a mean body weight for each size class, the percent of total body weight consumed daily was calculated based on the equations of Francis (1983). This total biomass consumption was then broken down into the constituent prey categories found in the stomachs of fish sampled using the percent of the diet by weight. These calculations were repeated for each of the five classes, and both the pelagic and benthic components of the population, to derive daily consumption estimates.

Residence times provided by Francis (1983) for each age class within each statistical area were converted to residence time by size class to account for the migratory behavior of Pacific hake. This provided consumption rate estimates summed over the length of time Pacific hake are found in the Columbia statistical area. An example of the calculations used to estimate total consumption of each prey item category is shown in Table 1.

Pacific Hake-Pink Shrimp Interaction

The relationship between the abundance of Pacific hake and pink shrimp was examined via regression analysis. Data from Francis et al. (unpubl. data) on Pacific hake catches in U.S. waters from 1967 to 1982 were converted to catch per unit effort (CPUE) based on the number of days of effort of foreign stern-trawling factory ships (BMRTs). Pounds per hour of pink shrimp taken in the equivalent of single-rigged shrimp trawls (SRE) in California, Washington, and Oregon from 1968 to 1984 (Saelens and Zirges 1985) were used as the dependent variable in regression analyses.

Two regressions were performed. The first used hake CPUE in year i to predict shrimp CPUE in year i, while the second involved a 2-yr lag (i.e., Pacific hake CPUE in year i versus shrimp CPUE in year $i + 2$).

TABLE 1.—Calculations used to compute total consumption of *Thysanoessa spinifera*. Column E1 = A × B/100 × C/100. Column E2 = E1 × D. Biomass is combined benthic and pelagic components of the population, BWD is percent body weight consumed per day, W is percent of the diet by weight composed of *T. spinifera*, and Days is number of days each size class resides in the Columbia INPFC Area. Note total biomass differs from value given in text due to biomass of population <35 cm in length.

Size class (cm)	(A) Biomass (1,000 t)	(B) %BWD	(C) %W	(D) Days	(E1) Consumption Daily	(E2) Consumption Seasonal (1,000 t)
35-39	331.252	1.10	14.7	80	0.540	42.85
40-44	69.126	0.98	9.4	69	0.060	4.20
45-49	21.272	0.84	17.2	45	0.030	1.38
50-54	17.640	0.65	14.9	42	0.020	0.72
55+	8.936	0.40	6.4	41	0.002	0.09
Total	448.226				0.652	49.24

RESULTS

Stomach Content Analysis

A breakdown of the stomach contents by size class of Pacific hake is presented in Table 2. Euphausiids dominate the diet of small hake while decapods and fish become increasingly important as Pacific hake increase in size. Considering percent of the diet by weight, the importance of euphausiids monotonically decreases from 100 to 7.9% with increasing predator size. Likewise, the importance of fish rises from 0 to 87.1% with increasing predator size. Pink shrimp comprise only a minor portion of the diet, the largest percentage being 4.9% for the largest size class. Commercially important herring comprise nearly one-third of the diet of the larger size classes.

A previously unreported prey item, the ghost shrimp, *Callianassa* sp., appeared in the diet of the Pacific hake sampled in this study. These burrow-

TABLE 2.—Summary of stomach contents of *Merluccius productus* collected during the 1983 NMFS Pacific Coast Groundfish Survey. T = <0.1%.

Prey category	30-34 cm			35-39 cm			40-44 cm			45-49 cm			50-54 cm			>55 cm		
	FO[1]	%N[2]	%W[3]	FO	%N	%W	FO	%N	%W	FO	%N	%W	FO	%N	%W	FO	%N	%W
Euphausiacea																		
Thysanoessa spinifera	—	—	—	14.9	15.0	14.7	27.5	10.6	9.4	32.5	79.6	17.2	52.4	65.1	14.9	61.9	62.3	6.4
Euphausia pacifica	25.0	16.7	17.1	56.4	73.7	72.7	68.1	78.5	70.8	10.4	9.0	2.2	19.5	18.7	3.9	33.3	23.4	1.3
Unidentified	100.0	83.3	82.9	33.0	10.4	6.2	33.3	10.3	10.7	31.2	9.2	2.5	35.4	12.4	1.9	19.0	9.0	0.2
Decapoda																		
Pandalus jordani	—	—	—	1.1	T	0.2	—	—	—	1.3	0.1	0.1	—	—	—	19.0	2.3	4.9
Sergestes similis	—	—	—	2.1	0.7	2.9	5.8	0.3	2.5	—	—	—	—	—	—	—	—	—
Pasiphaea pacifica	—	—	—	—	—	—	1.5	T	2.0	—	—	—	—	—	—	14.3	1.5	0.4
Crangon sp.	—	—	—	—	—	—	—	—	—	2.6	0.1	0.2	4.9	1.1	12.0	—	—	—
Callianassa sp.	—	—	—	—	—	—	—	—	—	11.7	0.7	13.4	8.5	1.1	14.5	—	—	—
Osteichthyes																		
Engraulis mordax	—	—	—	—	—	—	—	—	—	1.3	0.1	1.5	2.4	0.3	2.7	—	—	—
Clupea harengus	—	—	—	—	—	—	2.9	0.1	3.8	3.9	0.2	34.7	3.7	0.2	28.4	—	—	—
Thaleichthys pacificus	—	—	—	—	—	—	1.4	T	0.6	9.1	0.4	23.0	1.2	0.1	T	—	—	—
Osmeridae	—	—	—	—	—	—	—	—	—	1.3	0.1	T	1.2	0.1	2.8	—	—	—
Gadidae	—	—	—	—	—	—	—	—	—	1.3	0.1	1.2	2.4	0.2	2.4	4.8	0.2	83.6
Pleuronectidae	—	—	—	—	—	—	—	—	—	1.3	0.2	0.1	2.4	0.2	14.5	9.5	0.6	3.4
Agonidae	—	—	—	—	—	—	—	—	—	—	—	—	1.2	0.1	0.4	—	—	—
Myctophidae	—	—	—	0.8	T	1.5	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	—	—	—	5.3	0.2	1.8	5.8	0.2	0.3	9.1	0.4	3.6	7.3	0.5	1.8	14.3	0.6	0.1
Number of stomachs (empty)	11 (7)			120 (26)			97 (28)			118 (41)			93 (11)			27 (6)		
Number of prey items	6			2,006			2,029			1,921			1,206			478		
Weight of stomach contents (g)	0.4			77.0			78.0			376.5			319.3			293.0		

[1]Frequency of occurrence in non-empty stomachs.
[2]Percent of diet by number of items.
[3]Percent of diet by weight of stomach contents.

ing animals were found in stomachs of Pacific hake taken at towing stations between 8.3 and 15.6 km (4.5 and 8.5 mi) offshore but not in immediate proximity to estuaries where ghost shrimp are most often found.

Chi-square tests (Table 3) illustrate the patterns in prey consumption by various stratifications of the data. There was little statistical difference in stomach contents of males compared with females. The analysis of prey categories by depth is essentially an inshore-offshore comparison as isobaths run roughly parallel to the coastline in the study area. Statistically significant differences were found in depth of capture for both species of euphausiids found in this study. *Thysanoessa spinifera* was more important in the diet of fish taken close to shore whereas *Euphausia pacifica* was important for fish taken futher offshore. Eulachon, *Thaleichthys pacificus*, was found in stomachs more often in shallow waters than at depth. These animals, being anadromous, are often found in bays and estuaries, i.e., close to shore.

A significant difference exists in the presence of the two species of euphausiids in stomachs collected at different times of the day. The data collected in this study show that *T. spinifera* were seldom found in stomachs collected after 1600 h while *E. pacifica* were often found in stomachs collected during that time (Fig. 2a).

TABLE 3.—Chi-square analysis of difference in stomach content by prey category and various factors.

Prey category	Factor			
	Sex df = 1	Depth df = 2	Time df = 2	Size df = 4
Thysanoessa spinifera	2.48	15.65***	23.67***	36.69***
Euphausia pacifica	1.42	17.45***	6.23*	76.90***
Pandalus jordani	0.48	1.02	3.53	39.60***
Sergestes similis	0.02	28.07***	0.12	9.86*
Pasiphaea pacifica	0.80	17.47***	3.92	34.39***
Crangon sp.	0.02	6.40*	3.07	8.27
Callianassa sp.	0.05	3.69	9.14*	20.30***
Engraulis mordax	0.46	0.68	3.87	3.99
Clupea harengus	0.76	3.95	10.14**	4.30
Thaleichthys pacificus	0.72	9.35**	4.14	16.71**
Osmeridae	2.24	1.44	2.49	2.33
Gadidae	0.01	0.16	2.20	5.44
Pleuronectidae	4.55*	1.45	2.21	12.49*

* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

To further examine the diel feeding pattern of Pacific hake, the percent of all stomachs in each of two fullness categories (<25% full; > 75% full) was calculated by time of day. A three-point moving average was computed for each fullness category, and the resulting averages plotted (Fig. 3). There

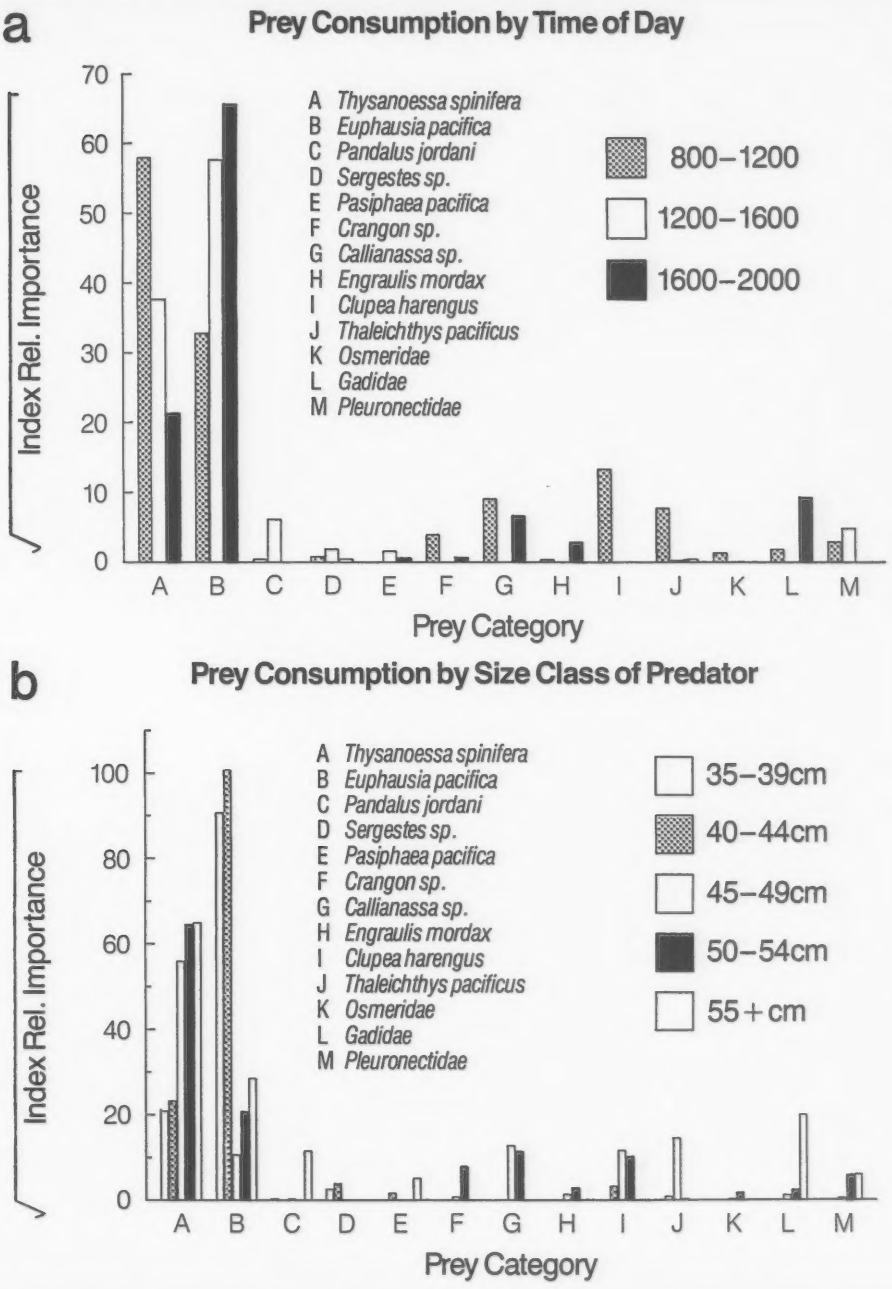

FIGURE 2.—Index of relative importance for major prey categories by a) time of collection and b) size of Pacific hake. Square root transformation used for scaling purposes.

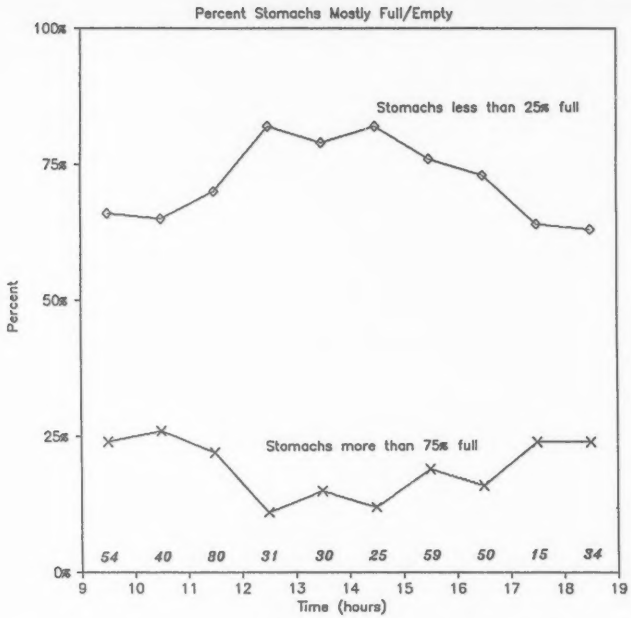

FIGURE 3.—Diel pattern of stomach contents of Pacific hake as demonstrated by percent of stomachs <25% full (upper curve) and >75% full (lower curve). Three-point moving average used to smooth the curves. Sample sizes shown above x-axis.

is a weak indication that these fish exhibit a pattern of feeding more heavily at night than during the day. For a predator feeding nocturnally, the expected pattern of this curve would be low percentages of empty stomachs early and late in the day, and high percentages of empty stomachs at midday. No tows were made between the hours of 2000 and 0700 thus direct evidence of nocturnal feeding was not available.

Comparison of stomach contents by size class showed the greatest amount of variation (Table 3, Fig. 2b) because of the shift in diet composition from euphausiids in early life stages to fishes in later stages.

The estimated consumption by Pacific hake in the Columbia statistical area over all prey categories is 4,651 t/d (Table 4). The amount of euphausiids consumed (over 4 kt/d), exceeds that of all other prey categories combined, but several commercially valuable species are also consumed in significant quantities. Consumption of pink shrimp is estimated at over 9.2 t/d, and almost 120 t/d of herring are consumed. Residence time for each size class of Pacific hake was derived from data presented by Francis (1983) (size class 1: 80 d; size class 2: 69 d; size class 3: 45 d; size class 4: 42 d; and size class 5: 41 d) to extrapolate estimates of annual prey consumption from the daily consumption rate in the Columbia area. The annual consumption of pink shrimp, based on these data, is estimated at 659.3 t.

Pacific Hake-Pink Shrimp Interaction

The regression of Pacific hake CPUE versus pink shrimp CPUE resulted in a nonsignificant correlation (r^2 = 0.114, df = 15, P = 0.185). However, the regression performed with a 2-yr lag (hake CPUE in year i versus shrimp CPUE in year i + 2) showed a significant negative correlation between the variables (r^2 = 0.418, df = 15, P = 0.005). Note that the significance of the latter analysis stems largely from data obtained in recent years (Fig. 4).

DISCUSSION

One of the most striking patterns found in the data is the distinct change in diet composition that Pacific

TABLE 4.—Diet composition by size class on a daily basis (t) and on seasonal basis (kt). Values based on biomass for the Columbia INPFC area estimated from bottom trawl survey (Weinberg et al. 1984) and hydroacoustic survey (Francis, see text fn. 4). T – <0.1 t/d or 0.05 kt seasonally.

	Size 1		Size 2		Size 3		Size 4		Size 5		Totals	
Prey category	Daily	Season	Daily	Season	Daily	Season	Daily	Season	Daily	Season	Daily	Season
Euphausiacea												
Thysanoessa spinifera	535.1	42.5	64.0	4.4	30.6	1.4	17.2	0.7	2.3	.0.1	649.2	49.1
Euphausia pacifica	2,646.4	210.4	481.8	33.2	3.9	0.2	4.5	0.2	0.5	T	3,137.1	244.0
Unid. euphausiid	225.7	17.9	72.8	5.0	4.5	0.2	2.2	0.1	0.1	T	305.2	23.3
Total euphausiid	3,407.3	270.9	618.6	42.7	39.0	1.7	23.9	1.0	2.8	0.1	4,091.6	316.4
Decapoda												
Pandalus jordani	7.3	0.6	0.0	0.0	0.2	T	0.0	0.0	1.8	0.1	9.2	0.7
Sergestes sp.	105.6	8.4	17.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	122.6	9.6
Pasiphaea pacifica	0.0	0.0	13.6	0.9	0.0	0.0	0.0	0.0	0.1	T	13.8	1.0
Crangon sp.	0.0	0.0	0.0	0.0	0.4	T	13.8	0.6	0.0	0.0	14.2	0.6
Callianassa sp.	0.0	0.0	0.0	0.0	23.9	1.1	16.7	0.7	0.0	0.0	40.6	1.8
Osteichthyes												
Engraulis mordax	0.0	0.0	0.0	0.0	2.7	0.1	3.1	0.1	0.0	0.0	5.8	0.2
Clupea harengus	0.0	0.0	25.9	1.8	61.8	2.8	32.8	1.4	0.0	0.0	120.5	5.9
Thaleichthys pacificus	0.0	0.0	4.1	0.3	41.0	1.8	0.1	T	0.0	0.0	45.1	2.1
Osmeridae	0.0	0.0	0.0	0.0	0.4	T	3.2	0.1	0.0	0.0	3.6	0.2
Gadidae	0.0	0.0	0.0	0.0	2.1	0.1	2.8	0.1	30.2	1.2	35.1	1.4
Pleuronectidae	0.0	0.0	0.0	0.0	0.2	T	16.7	0.7	1.2	0.1	18.1	0.8
Agonidae	0.0	0.0	0.0	0.0	0.0	0.0	0.5	T	0.0	0.0	0.5	T
Myctophidae	54.6	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	54.6	4.3
Unid. fish	65.5	5.2	2.0	0.1	6.4	0.3	2.1	0.1	T	T	76.1	5.7
Grand total	3,640.2	289.4	681.2	47.0	178.0	8.0	115.7	4.8	36.2	1.5	4,651.4	350.7

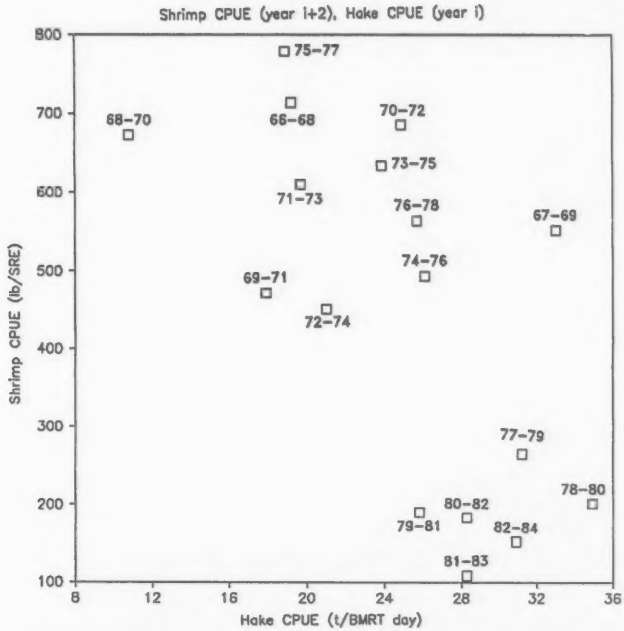

FIGURE 4.—Pink shrimp CPUE in year $i + 2$ (y-axis) plotted against Pacific hake CPUE in year i (x-axis). Regression expression is $y = 1029 - 23.23x$ ($r^2 = 0.418$). Numbers on the plot represent the years of the CPUE data.

hake undergo as they increase in size. *Thysanoessa spinifera* appears to be more important to larger hake whereas *Euphausia pacifica* is more important to smaller individuals. Pink shrimp and glass shrimp, *Pasiphaea pacifica*, were consumed almost exclusively by fish >55 cm. Eulachon and pleuronectids were also predominantly consumed by larger hake. Cannibalism was also observed among larger individuals.

Diel Feeding Pattern

A number of previous researchers have postulated that species in the genus *Merluccius* exhibit a diel feeding pattern (Outram and Haegele 1972; Bowman and Bowman 1980). Alton and Nelson (1970) as well as Livingston (1983) described Pacific hake as nocturnal predators that migrate vertically to feed near the surface during hours of darkness and dive to deeper water during daylight hours. Brinton (1967) and Alton and Blackburn (1972) showed that this same vertical migration pattern exists for the two species of euphausiids found in this study. If the Pacific hake follow the euphausiids on their vertical diel migration, the expectation is that the relative proportion of both species of euphausiids in the diet should not vary significantly by time of day. As reported above, our findings conflict with this expectation.

To further examine this apparent deviation, we considered potentially confounding factors; such as differences in the distributions of the euphausiid species and various size classes of Pacific hake. Brinton (1962) reported that *T. spinifera* is a neritic species and *E. pacifica* is a more oceanic species. Analysis of length-frequency data from the cruise during which this study was conducted shows that Pacific hake of different size classes segregate by depth. Pacific hake <40 cm in length made up 37% of the catch in <100 m of water, but these same size classes comprised 62% of the catch taken in >100 m of water. Hence, the smaller individuals were found in greater abundance in the habitat associated with *E. pacifica*.

This phenomenon of smaller fish occurring in deeper water and consequently consuming greater quantities of *E. pacifica* explains the apparent difference in importance of the two species of euphausiids by time of day (Fig. 2a). Only 7% of the nonempty stomachs taken before 1200 h were from fish <40 cm in length whereas of the fish sampled after 1600 h, 34% were <40 cm in length. Thus, we regard the observed differences in consumption of *T. spinifera* and increasing importance of *E. pacifica* by time of day as spurious, confounded by the differences in the diets and distributions of various size classes of Pacific hake.

This study coincided with the strong presence of El Niño in 1983 which may have altered the normal migration pattern of Pacific hake and consequently the residence time estimates, and may also have affected the abundance of the prey base. Hence, there may be some error in the consumption estimates presented herein. Miller et al. (1984) noted a decline in the relative abundance of *T. spinifera* off the Oregon coast during 1983 in comparison with other years. Thus, feeding to satiation during evening hours may have been impossible; consequently, feeding occurred whenever euphausiids were encountered. Additional circumstantial evidence of aberrant feeding behavior of Pacific hake in 1983 is their severely depressed growth (Francis and Hollowed 1985). Food resources may only have been sufficient for maintenance metabolism with little energy remaining for growth. These observations may explain why the diel feeding pattern observed was weak.

Trophic Interaction

The seasonal migration pattern and consequent latitudinal stratification of Pacific hake stocks by size class makes it difficult to compare food habit studies conducted at different times of the year and at different locations on the Pacific coast. Nonetheless, examining only the role of pink shrimp in the diet, we find first mention of Pacific hake preying on this species by Gotshall (1969a, b). Analyzing Pacific hake stomachs collected off California between 1966 and 1969, Gotshall found high incidences (54% frequency of occurrence) of pink shrimp during late summer and early fall, particularly in Pacific hake collected over shrimp beds. The study was an attempt to use Pacific hake as biological samplers to estimate pink shrimp abundance, focusing sampling effort on known pink shrimp beds, and, as such, the sampling design was quite different from other studies.

Outram and Haegele (1972) reported that 3% of the Pacific hake stomachs collected off the coast of British Columbia contained pink shrimp. Pink shrimp were found in 5.7% of the Pacific hake stomachs collected during the summers of 1965 and 1966 off Washington and Oregon (Alton and Nelson 1970). Livingston and Alton (1982) found that pandalid shrimp constituted 0.3% by weight of the contents of the 1,430 stomachs of Pacific hake taken off the coasts of Washington and Oregon during the

summer of 1967. From 204 stomachs collected during the 1980 NMFS West Coast Groundfish Survey off the coasts from Oregon to Vancouver Island, Livingston (1983) found pink shrimp constituted 0.7% by weight of the Pacific hake diet. Pink shrimp occurred in 1.7% of the Pacific hake stomachs collected in the study described in this paper. Thus, with the exception of Gotshall's work, studies of the food habits of Pacific hake have shown pink shrimp generally comprise well under 10% of the Pacific hake diet, and thus do not appear to be an important food source for hake. However, due to the large biomass of Pacific hake in the North Pacific, it is possible that Pacific hake may represent a significant source of mortality even for those species, including pink shrimp, that are not significant components of the Pacific hake diet (Francis 1983).

The estimated consumption of 659.3 t/season of pink shrimp compares with a commercial catch of 2,197 t of pink shrimp landed in Oregon during 1984 by 59 vessels (Saelens and Zirges 1985). It is conceivable that the magnitude of Pacific hake predation on pink shrimp may increase in the near future. Small Pacific hake, preying mainly on euphausiids, constituted the bulk of the consumers in this study. The strong 1980 year class of Pacific hake, seen as the 35-39 cm size class in these 1983 data, will have substantially greater impact on commercially valuable species upon reaching larger sizes when these valuable species comprise a larger fraction of the diet.

Francis (1983) inferred, from catch statistics of Pacific hake and pink shrimp, that increased catches of Pacific hake since the inception of the foreign and subsequent joint-venture fisheries may have contributed to the dramatic increase in the landings of pink shrimp during the late 1970s. The causal mechanism inferred is the release of predation pressure on the pink shrimp population as a result of decreased Pacific hake abundance due to fishing. This "surplus" in the pink shrimp population was harvested by the increasingly vigorous shrimp fishery.

This contention is disputed by Livingston and Bailey (1985). Their analysis focuses on pink shrimp CPUE during two time periods: 1952-65 during which Pacific hake were unexploited and 1966-77 during which a substantial joint-venture fishery occurred. They found no appreciable change in average pink shrimp CPUE between the two periods. Extending their analysis to include the most recent catch statistics, we also fail to find the existence of a significant difference between the periods 1957-65 and 1966-84 (t = 1.05, 26 df, P = 0.303).

However, if pink shrimp have constituted a fairly constant proportion of the Pacific hake diet over time, as suggested by this and previous Pacific hake food habit studies, then there may indeed be a relationship between the release of predator pressure by the Pacific hake and increased catches of pink shrimp. The regression-correlation analysis presented above has an advantage over the average pink shrimp CPUE analysis because it incorporates information about both hake and shrimp abundances. The regression-correlation results provide weak statistical support to Francis' contention that there is a relationship between Pacific hake and pink shrimp population dynamics. However, further observations are needed to obtain greater confidence in this relationship. In particular, it will be interesting to note that the impact of the strong 1980 year class Pacific hake on pink shrimp catches in the near future.

CONCLUSION

Pacific hake occupy a unique trophic position, serving not only as predators but also as prey for a variety of species carrying valuations other than those of an economic nature (endangered species and species managed under the Marine Mammal Protection Act). Euphausiids constitute the primary source of food for Pacific hake in the North Pacific. However, as Pacific hake mature, euphausiids decrease in importance and fish take on greater importance. Owing to the vast quantity of hake biomass living in the North Pacific, it has been shown that Pacific hake may consume large quantities of several commercially valuable species, even though these species comprise a fairly small percentage of the diet. It has also been demonstrated that a statistically significant relationship exists between CPUE of Pacific hake and pink shrimp. Additional years of data are required to have a clearer understanding of this relationship.

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LITERATURE CITED

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen in coastal waters of Washington. Calif. Fish Game 58:179-190.

ALTON, M. S., AND M. O. NELSON.
1970. Food of Pacific hake, *Merluccius productus*, in Washington and northern Oregon coastal waters. *In* Pacific hake, p. 35-42. U.S. Fish Wildl. Serv., Circ. 332.

BAILEY, K. M., R. C. FRANCIS, AND P. R. STEVENS.
1982. The life history and fishery of Pacific whiting, *Merluccius productus*. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 81-98.

BEST, E. A.
1963. Contribution to the biology of the Pacific hake, *Merluccius productus* (Ayres). Calif. Coop. Oceanic Fish. Invest. Rep. 9:51-56.

BOWMAN, R. E., AND E. W. BOWMAN.
1980. Diurnal variation in the feeding intensity and catchability of silver hake (*Merluccius bilinearis*). Can. J. Fish. Aquat. Sci. 37:1565-1572.

BRINTON, E.
1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8(2):51-269.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12: 451-483.

BRODEUR, R. D., AND W. G. PEARCY.
1984. Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the northeastern Pacific Ocean. Fish. Bull., U.S. 82:269-293.

FISCUS, C. H.
1979. Interactions of marine mammals and Pacific hake. Mar. Fish. Rev. 41(10):1-9.

FRANCIS, R. C.
1983. Population and trophic dynamics of Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 40:1925-1943.

FRANCIS, R. C., AND A. HOLLOWED.
1985. Status of the Pacific hake resource and recommendations for management in 1985. Status of stocks document to Pacific Fisheries Management Council, Portland, OR.

GOTSHALL, D. W.
1969a. Stomach contents of Pacific hake and arrowtooth flounder from northern California. Calif. Fish Game 55: 75-82.
1969b. The use of predator food habits in estimating relative abundance of the ocean shrimp, *Pandalus jordani* Rathbun. FAO Fish. Rep. 57, p. 667-685.

GUNDERSON, D. R., AND T. M. SAMPLE.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42 (3-4):2-16.

KARPOV, K. A., AND G. M. CAILLIET.
1978. Feeding dynamics of *Loligo opalescens*. *In* C. W. Recksiek and H. W. Frey (editors), Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry, p. 45-65. Calif. Dep. Fish Game, Fish Bull. 169.

LIVINGSTON, P. A.
1983. Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980. Fish. Bull. U.S. 81:629-636.

LIVINGSTON, P. A., AND M. S. ALTON.
1982. Stomach contents of Pacific whiting off Washington and Oregon, April-July 1967. U.S. Dep. Commer., NOAA Tech. Memo, NMFS F/NWC-32.

LIVINGSTON, P. A., AND K. M. BAILEY.
1985. Trophic role of the pacific Whiting, *Merluccius productus*. Mar. Fish. Rev. 47(2):16-22.

MILLER, C. B., H. P. BATCHELDER, R. D. BRODEUR, AND W. G. PEARCY.
1984. Response to the zooplankton and ichthyoplankton off Oregon to the El Niño event of 1983. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North: Nino effects in the eastern subarctic Pacific Ocean, p. 185-187. Wash. Sea Grant Prog., Univ. Wash., Seattle.

OSTLE, B., AND R. W. MENSING.
1975. Statistics in research. 3d ed. Iowa State Univ. Press, Ames, 596 p.

OUTRAM, D. N., AND C. HAEGELE.
1972. Food of Pacific hake (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia. J. Fish. Res. Board Can. 29:1792-1795.

PETERSON, W. T., R. D. BRODEUR, AND W. G. PEARCY.
1982. Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish. Bull., U.S. 80:841-851.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152: 1-105.

SAELENS, M. R., AND M. H. ZIRGES.
1985. The 1984 Oregon shrimp fishery. Oreg. Dep. Fish Wildl. Inf. Rep. 85-6.

SWARTZMAN, G. L., W. M. GETZ, R. C. FRANCIS, R. T. HAAR, AND K. ROSE.
1983. A management analysis of Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40(4):524-539.

TYLER, H. R., JR., AND W. G. PEARCY.
1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. Mar. Biol. (Berl.) 32:7-11.

WEINBERG, K. L., M. E. WILKINS, AND T. A. DARK.
1984. The 1983 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, age and length composition. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-70.

DIET OF NORTHERN FUR SEALS, *CALLORHINUS URSINUS*, OFF WESTERN NORTH AMERICA

MICHAEL A. PEREZ[1] AND MICHAEL A. BIGG[2]

ABSTRACT

Data recorded from the stomach contents of 18,404 northern fur seals, *Callorhinus ursinus*, mostly females aged ≥3 years collected off western North America during 1958-74, were analyzed to determine the relative importance of each prey species by region, subregion, and month. When weighted for energy content, the primary food species were small schooling fishes. Between western Alaska and California from December to August the most significant prey species were northern anchovy, *Engraulis mordax* (20%); Pacific herring, *Clupea harengus pallasi* (19%); capelin, *Mallotus villosus* (8%); Pacific sand lance, *Ammodytes hexapterus* (8%); Pacific whiting, *Merluccius productus* (7%); salmon, *Oncorhynchus* spp. (6%); Pacific saury, *Cololabis saira* (4%); and rockfishes, *Sebastes* spp. (4%). Other food species eaten in this area consisted of a wide variety of squids (17%) and other fishes (7%). In the eastern Bering Sea the main prey species from June to October were juvenile walleye pollock, *Theragra chalcogramma* (35%); capelin (16%); Pacific herring (11%); and squids, *Berryteuthis magister* and *Gonatopsis borealis*, which comprise most (30%) of the remaining diet of northern fur seals in this region. In all areas off western North America, fishes were the main food species of these pinnipeds in neritic waters, while squids were the most important prey in oceanic waters. Typically three prey species comprised 80% of their diet in any one area, although the composition of the diet varied in type and importance by region and month.

The northern fur seal, *Callorhinus ursinus*, is found in the Bering Sea, Sea of Okhotsk, and throughout the North Pacific Ocean, north of approximately lat. 32°N off western North America and lat. 36°N off Asia (Baker et al. 1970; Fiscus 1978). Although its pelagic distribution is extensive, the main concentrations lie over the continental shelf. There are three main stocks of this species. The largest stock breeds on the Pribilof Islands in the eastern Bering Sea and migrates primarily to coastal waters between the Gulf of Alaska and California. The other two stocks breed on the Commander Islands in the western Bering Sea and on Robben Island off northern Japan. Both stocks migrate primarily along the Asian coast. To determine the diet of the Pribilof Islands population, the United States and Canada, under the auspices of the North Pacific Fur Seal Commission, conducted annual pelagic studies during 1958-74 to collect stomach contents and other biological information.

The results of research on the diet of northern fur seals by the United States and Canada during 1958-74 have been presented in many annual and 2-6 yr summaries submitted by each country to the North Pacific Fur Seal Commission. Kajimura (1984) cited most of these reports. Spalding (1964), Stroud et al. (1981), and Kajimura (1985) also published reports on diet collected since 1958. Studies on the food habits of the northern fur seal prior to 1958 include Lucas (1899), Clemens and Wilby (1933), Clemens et al. (1936), Schultz and Rafn (1936), May (1937), Wilke and Kenyon (1952, 1954, 1957), Taylor et al. (1955), and Kenyon (1956).

Investigations to date have reported that northern fur seals eat a wide variety of fishes and squids. However, the relative importance of each prey species has remained uncertain because substantial differences often existed between values of relative importance derived by volumetric measure and those derived by frequency of occurrence. For example, squids were important (averaging 39%) in the diet using frequency of occurrence but not significant (15%) using volume (Bigg and Fawcett 1985; Perez and Bigg[3]). The long-suspected reason for this difference was that squid beaks accumulated

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[3]Perez, M. A., and M. A. Bigg. 1980. Interim report on the feeding habits of the northern fur seal in the eastern North Pacific Ocean and eastern Bering Sea. *In* H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg, Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, Part 2, p. 4-172. Unpubl. rep. Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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in stomachs of seals thereby inflating the importance of squid (Scheffer 1950; Spalding 1964; Bigg and Fawcett 1985). Recent experimental studies confirmed that squid beaks accumulate in fur seal stomachs (Bigg and Fawcett 1985).

To date, no reports have been published on the diet of northern fur seals that take this bias into account. However, Bigg and Perez (1985) suggested a method, called modified volume, which reduces the bias and also accounts for differences in digestion rates between fish and squid. In this method, evidence of diet based on trace remains, such as squid beaks and fish bones, is omitted in the analyses, and a combination of the frequency of occurrence and volumetric methods is used to establish the relative importance of individual prey species.

We use the modified volume method in this report to analyze data from the stomach contents collected by the United States and Canada during 1958-74. We will describe the annual diet of northern fur seals in the eastern North Pacific and eastern Bering Sea by region and subregion. We also incorporate the energy content of important prey species to determine whether this might affect relative importance, a procedure not tried previously with this seal.

METHODS

Lander (1980) and Kajimura (1984, 1985) described the methods used to take northern fur seals at sea during 1958-74 and to identify and measure the prey items found in their stomachs by volume and frequency of occurrence. A total of 18,404 stomachs were collected of which 7,373 contained food and an additional 3,326 had only trace remains. Perez and Bigg (fn. 3) summarized the data on volume and frequency of occurrence for all species of northern fur seal prey by month and region.

Perez and Bigg[4] and Bigg and Perez (1985) gave a detailed discussion of the procedure used to calculate modified volume values. First, prey species represented in any stomach only by trace amounts (≤10 cc) were omitted. Second, the proportions of total fish and total squid in the diet by subregion, region, and month were then determined by non-trace frequency of occurrence. Third, the ratio of each species within only the fish category and within only the squid category was determined by volume. The taxonomic groupings recorded in the original data which overlapped each other were either pooled with higher taxa or were proportionally divided among component species depending upon which level of taxa had the most data. This prevented food groupings from being partially compared against themselves. Next, the volumetric ratios for individual fish and squid species were adjusted to sum, respectively, to the total proportion of fish and squid in the diet. Finally, all values were readjusted to total 100%.

The relative importance of prey species has been presented in this report in two ways: 1) modified volume values for each region by month, and for each subregion with data from all months pooled; and 2) modified volume values for each region based on combined months data which were weighted for

TABLE 1.—Estimated energy values (wet mass) for important northern fur seal prey. C = bomb calorimetry combustion value; P = proximate analysis value[1]; muscle = edible portion only of raw material; whole = raw material from entire specimen.

Prey	Energy value (kcal/g)	Analysis and tissue	Reference
American shad	2.08	P, muscle	Sidwell (1981)
Pacific herring	2.17	P, whole	Sidwell (1981); Bigg et al. (1978)
Northern anchovy	1.79	P, whole	Sidwell (1981)
Salmonids	2.01	P, muscle	Sidwell (1981)
Capelin	1.31	C, whole	Miller[2]
Eulachon	1.41	P, muscle	Stansby (1976)
Deep-sea smelts	0.76	P, whole	Childress and Nygaard (1973)
Myctophiform fishes	1.58	P, whole	Childress and Nygaard (1973)[3]
Pacific saury	2.20	P, muscle	Sidwell (1981)
Jacksmelt	1.24	P, muscle	Watt and Merrill (1963)
Pacific cod	1.00	P, muscle	Sidwell (1981)
Pacific whiting	1.17	P, whole	Sidwell (1981)
Walleye pollock	1.41	C, whole	Miller[2]
Threespine stickleback	1.15	C, whole	Wootton (1976)
Jack mackerel	1.24	P, whole	Sidwell (1981)
Rockfishes	1.17	P, muscle	Sidwell et al. (1974)
Sablefish	2.17	P, muscle	Sidwell (1981)
Atka mackerel	1.58	P, muscle	Kizevetter (1971)
Pacific sand lance	1.22	P, muscle	Sidwell (1981)
Flounders	1.20	P, muscle	Sidwell (1981)[4]
Market squid	1.15	P, muscle	Sidwell (1981)
Onychoteuthid squids	1.29		Perez[5]
Gonatid squids	1.27		Perez[5]

[1]Values were calculated with the following energy factors derived from Watt and Merrill (1963): 9.50, 5.65 and 4.00 kcal/g respectively for fat, protein and carbohydrate.

[2]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Mar. Mammal Comm. Rep. MMC-75/08, 27 p.

[3]Myctophidae and Paralepididae.

[4]Pleuronectidae.

[5]Perez, M. A., Natl. Mar. Mammal Lab., Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, unpubl. data, 1984.

[4]Perez, M. A., and M. A. Bigg. 1981. Modified volume: a two-step frequency-volume method for ranking food types found in stomachs of northern fur seals. Unpubl. rep., 25 p. Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

the energy value of prey. Data from all years of collection were pooled. We assumed that the importance of a prey species to northern fur seals depended, at least in part, on its energy content. Table 1 lists the estimated caloric values for prey species consumed most often. These estimates are provisional because little is known about changes in energy content within each species by season. Energy values for squids tend to be lower than those for fishes, although large variability exists among fish species.

No attempt was made to describe diet by age, sex, and reproductive condition. In our sample, 88% of the northern fur seals were females aged ≥3 yr, of which 53% were pregnant and 29% were nonpregnant. Thus, the diet described is primarily that for pregnant and nonpregnant females aged ≥3 yr.

The eastern North Pacific Ocean and eastern Bering Sea were divided into 7 regions and 21 subregions (Fig. 1). The boundaries for the seven regions were those which have been traditionally

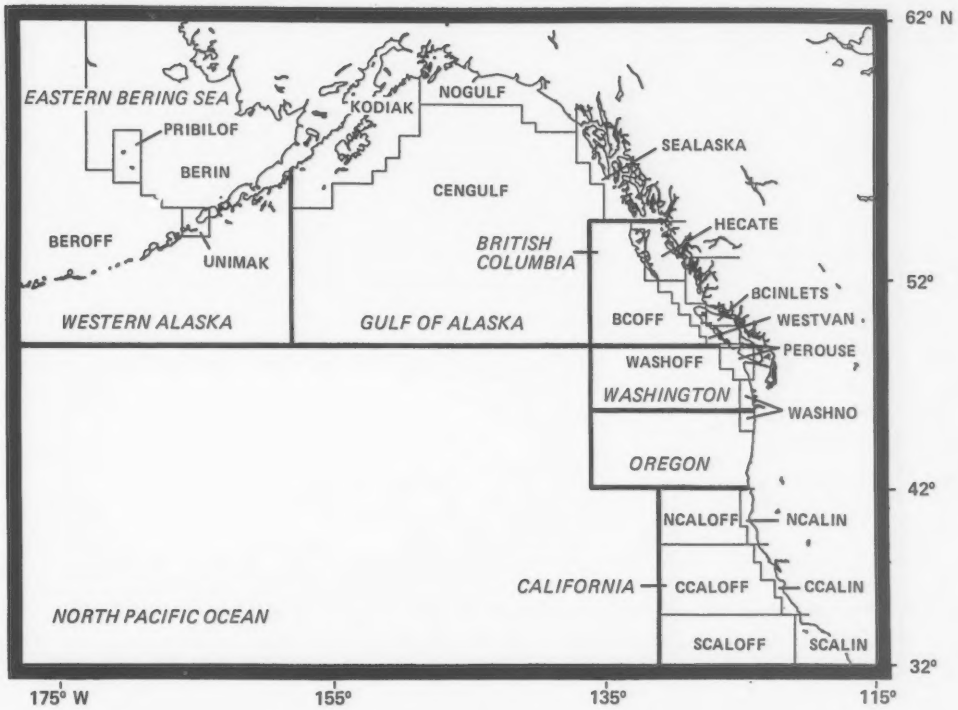

FIGURE 1.—Seven regions (denoted by darker lines) and 21 subregions used in the northern fur seal analyses: 1) California comprised of subregions SCALIN (southern California, inshore), SCALOFF (southern California, offshore), CCALIN (central California, inshore), CCALOFF (central California, offshore), NCALIN (northern California, inshore), and NCALOFF (northern California, offshore); 2) Oregon which includes half of subregion WASHNO (southern Washington and northern Oregon, inshore); 3) Washington which includes subregions PEROUSE (area west of Juan de Fuca Strait from Barkley Sound to Cape Flattery, including La Perouse Bank and Swiftsure Bank; inshore), WASHOFF (Washington, offshore), and half of WASHNO; 4) British Columbia which includes subregions BCINLETS (inside passages and inlets of B.C., inshore), WESTVAN (area west of Vancouver Island and Queen Charlotte Strait, inshore), HECATE (Hecate Strait area, inshore), and BCOFF (British Columbia, offshore); 5) the Gulf of Alaska which includes subregions SEALASKA (southeast Alaska, inshore), NOGULF (northern Gulf of Alaska, including Fairweather Bank; inshore), KODIAK (area around Kodiak Island, including Portlock Bank and Albatross Bank; inshore), and CENGULF (oceanic region of the Gulf of Alaska, offshore); 6) western Alaska which includes part of subregion UNIMAK (Unimak Pass area); and 7) the eastern Bering Sea comprised of subregions BERIN (Bering Sea shelf, inshore) and BEROFF (Bering Sea basin, offshore), and also includes subregions PRIBILOF (area around the Pribilof Islands) and most of UNIMAK. Subregions in which ≥50% of the area is ≤100 fathoms are noted as inshore; the remainder are noted as offshore.

used in analyses of pelagic data for northern fur seals. The subregions were selected to compare diet between inshore (neritic) and offshore (oceanic) areas and to indicate diet in certain localities where collection effort was relatively high. Inshore areas were defined as those generally occurring on the continental shelf (depths up to 100 fathoms) and offshore areas as those beyond the continental shelf.

RESULTS

The cruise tracks (Fig. 2) taken by research vessels of the United States and Canada for the collection of northern fur seals during 1958-74 indicate the relative distribution of research effort. Most collections were made in the coastal areas between California and British Columbia, off Kodiak Island, and in the eastern Bering Sea between Unimak Pass and the Pribilof Islands. Few specimens were taken more than 160 km from shore.

Diet by Region and Month

An examination of the number of prey species that made up the diet indicates that at least nine species may be consumed within any one subregion. However, typically only three prey species made up about 80% of the diet (Fig. 3). Thus, relatively few species of food are of primary importance in any one locality. As will be made clear in the following regional and subregional accounts, the primary food species can change among localities.

Our interpretation of Figures 4-11 which follow requires clarification. These figures show modified volume values only for those individual species that we felt were important and that had sufficient sample sizes to be reliable. Thus, we arbitrarily presented only those species that were of ⩾5% in importance for samples with at least 20 stomachs containing food. Species of less importance were pooled either as miscellaneous fishes or squids. Also, be-

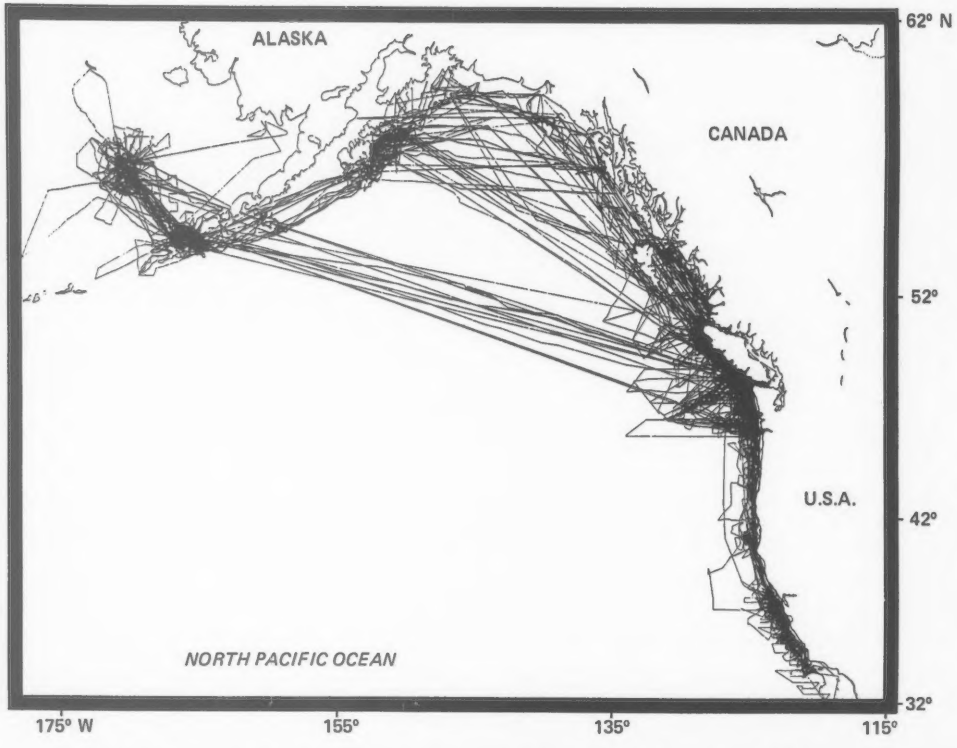

FIGURE 2.—Cruise tracks of northern fur seal research vessels from the United States and Canada during 1958-74.

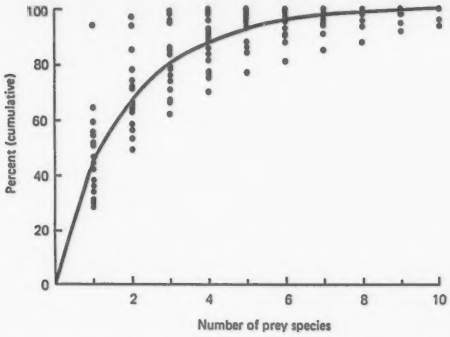

FIGURE 3.—The cumulative percentage distribution of the number of prey species eaten in the total diet of northern fur seals taken during 1958-74. Data for each of the 21 subregions are plotted, although only the average relationship is graphed.

cause the prey consumed by month within subregions were not presented here, we take these data from Perez and Bigg[5] in our interpretation of subregional data.

California

Northern anchovy, *Engraulis mordax*, was the most important food eaten by the northern fur seals off California (Fig. 4A) whether its energy content was considered or not. However, it was more important when its caloric value was taken into account. Northern anchovy was eaten mainly during January to March in inshore and offshore waters of central and southern California (Fig. 4B, C). Pacific whiting, *Merluccius productus*, was second in importance (Fig. 4A) and was preyed upon in all areas of California, although primarily during April and May (Fig. 4B, C). Market squid, *Loligo opalescens*, was eaten from January to June, but only in neritic locations (Fig. 4B, C). Onychoteuthid squids (Onychoteuthidae) were eaten offshore and were the more important squid species consumed in the southern areas off California (Fig. 4C). Other prey types were of relatively minor importance, although some were locally significant, such as Pacific saury, *Cololabis saira*, mainly in oceanic areas off northern and central California (Fig. 4A, B, C).

[5]Perez, M. A., and M. A. Bigg. 1981. An assessment of the feeding habits of the northern fur seal in the eastern North Pacific Ocean and eastern Bering Sea. Unpubl. draft rep., 146 p. Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

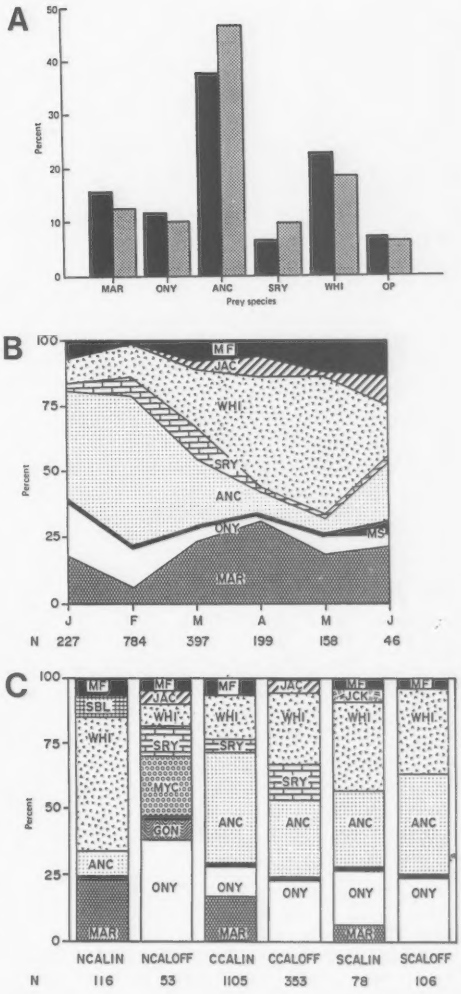

FIGURE 4.—Composition (percent) of diet of northern fur seals by prey species off California during 1958-74 (A) for pooled January-June samples (N = 1,811), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled January-June samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: ANC = northern anchovy; GON = gonatid squids; JAC = jack mackerel; JCK = jacksmelt; MAR = market squid; MF = miscellaneous fish species; MS = miscellaneous squid species; MYC = myctophiform fishes; ONY = onychoteuthid squids; OP = other prey; SBL = sablefish; SRY = Pacific saury; WHI = Pacific whiting.

Oregon

Only 69 northern fur seals with food in their stomachs were collected in Oregon between January and May during 1958-74, with 58 of these taken during April. Thus, diet could not be determined by month or by inshore and offshore areas. As in California, the main food was northern anchovy (Fig. 5). Other important prey were market squid, onychoteuthid squids, Pacific whiting, and rockfishes (*Sebastes* spp.).

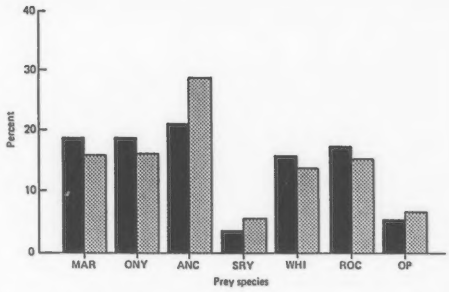

FIGURE 5.—Composition (percent) of diet of northern fur seals by prey species off Oregon during 1958-74 for pooled January-June samples (N = 69), using modified volume (dark bars) and energy-adjusted modified volume. Key: ANC = northern anchovy; MAR = market squid; ONY = onychoteuthid squids; OP = other prey; ROC = rockfishes; SRY = Pacific saury; WHI = Pacific whiting.

Washington

Pacific herring, *Clupea harengus pallasi*, was the most important food for northern fur seals off Washington, particularly when energy content was considered (Fig. 6A). It was only slightly more significant than rockfishes, salmonids (Salmonidae, primarily *Oncorhynchus* spp.), and northern anchovy when caloric values were not incorporated. Pacific herring was eaten from December to June but only

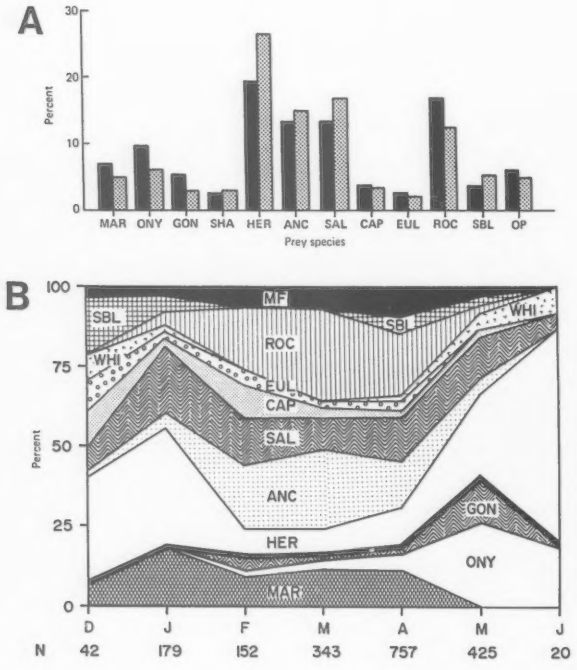

FIGURE 6.—Composition (percent) of diet of northern fur seals by prey species off Washington during 1958-74 (A) for pooled December-June samples (N = 1,918), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled December-June samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: ANC = northern anchovy; CAP = capelin; EUL = eulachon; GON = gonatid squids; HER = Pacific herring; MAR = market squid; MF = miscellaneous fish species; MS = miscellaneous squid species; ONY = onychoteuthid squids; OP = other prey; ROC = rockfishes; SAL = salmonids; SBL = sablefish; SHA = American shad; WHI = Pacific whiting.

in neritic areas (Fig. 6B, C). Rockfishes, salmonids, and northern anchovy were also consumed by seals during this time, both inshore and offshore. Northern anchovy was primarily important in the southern area of the region (Fig. 6C). The main food in oceanic waters consisted of two families of squids, Onychoteuthidae and Gonatidae (Fig. 6C). Market squid was the primary squid species preyed upon in neritic areas.

British Columbia

As in Washington, Pacific herring was the primary food of the northern fur seals from February to June in most inshore areas, particularly when energy content was taken into account (Fig. 7A, B, C). It was mainly consumed by northern fur seals off the west coast of Vancouver Island and in Hecate Strait. In coastal inlets, market squid was important, but not significantly for the region as a whole. The diet of northern fur seals in oceanic waters during May and June was almost exclusively onychoteuthid squids and salmonids (Fig. 7B, C). Other prey species were relatively insignificant (Fig. 7A). However, because the coastline of British Columbia is complex, and sample sizes were small, additional local differences in diet may exist in inshore areas (Fig. 7C).

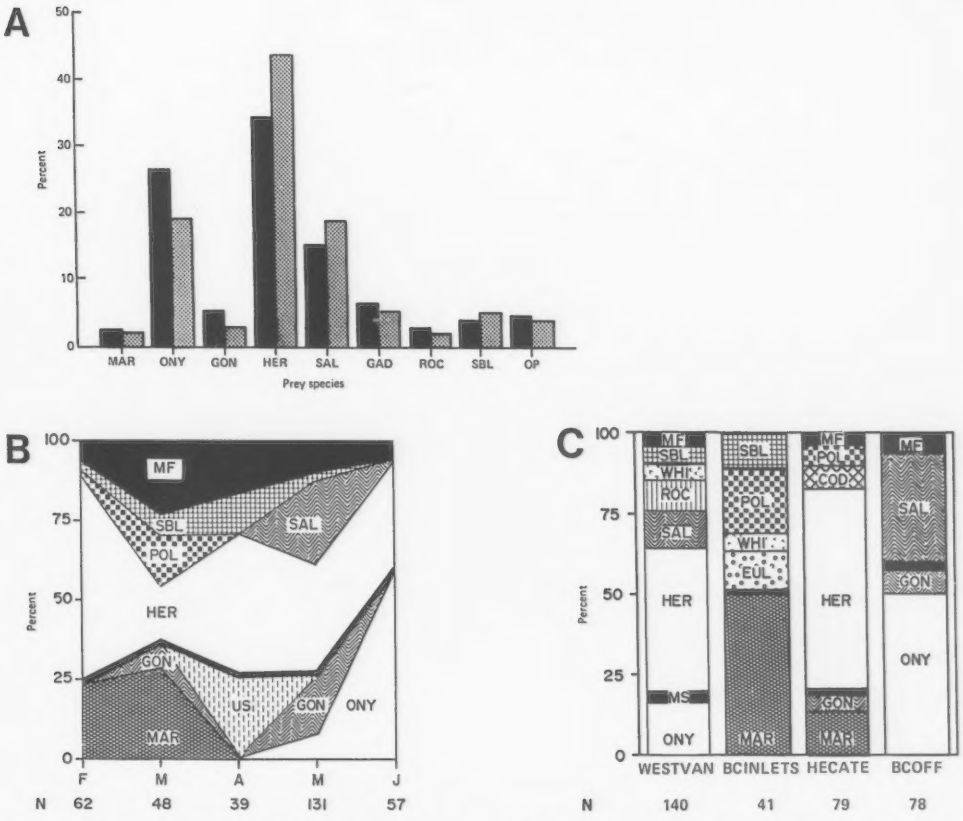

FIGURE 7.—Composition (percent) of diet of northern fur seals by prey species off British Columbia during 1958-74 (A) for pooled January-June samples (N = 354), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled January-June samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: COD = Pacific cod; EUL = eulachon; GAD = gadid fishes; GON = gonatid squids; HER = Pacific herring; MAR = market squid; MF = miscellaneous fish species; ONY = onychoteuthid squids; OP = other prey; POL = walleye pollock; ROC = rockfishes; SAL = salmonids; SBL = sablefish; US = unidentified squid; WHI = Pacific whiting.

Gulf of Alaska

Based on all samples collected in the Gulf of Alaska, the main diet of northern fur seals was Pacific herring when energy content was considered, but Pacific sand lance, *Ammodytes hexapterus*, was most important when caloric values were not considered (Fig. 8A). However, there were subregional differences in diet. Off southeastern Alaska, collections were made in Sitka Sound during February and March where the diet was almost exclusively Pacific herring (Fig. 8B, C). In the northernmost area of the region the diet consisted chiefly of capelin, *Mallotus villosus*, but also to a lesser degree of both walleye pollock, *Theragra chalcogramma*, and Pacific sand lance (Fig. 8C). Off Kodiak Island during April to July, the diet was mainly Pacific sand lance and capelin (Fig. 8B, C). Gonatid squids (Gonatidae) were the primary foods of northern fur seals in oceanic waters of this region from April to June. Rockfishes and salmonids were also eaten by northern fur seals in offshore and northern inshore areas of the region (Fig. 8C).

Western Alaska

Of the 309 stomachs with food collected in this region from May to October 1958-74, 239 were taken during June, with most of these collected south of Unimak Pass. The main foods of the northern fur seals were Pacific sand lance and capelin, as off Kodiak Island, with the energy content of each having little effect on their relative importance (Fig. 9). Other important prey were Atka mackerel, *Pleurogrammus monopterygius*, salmonids, walleye pollock, and the squid *Berryteuthis magister*. Sablefish, *Anoplopoma fimbria*, and Pacific herring were also eaten by northern fur seals south of Unimak Pass during summer months.

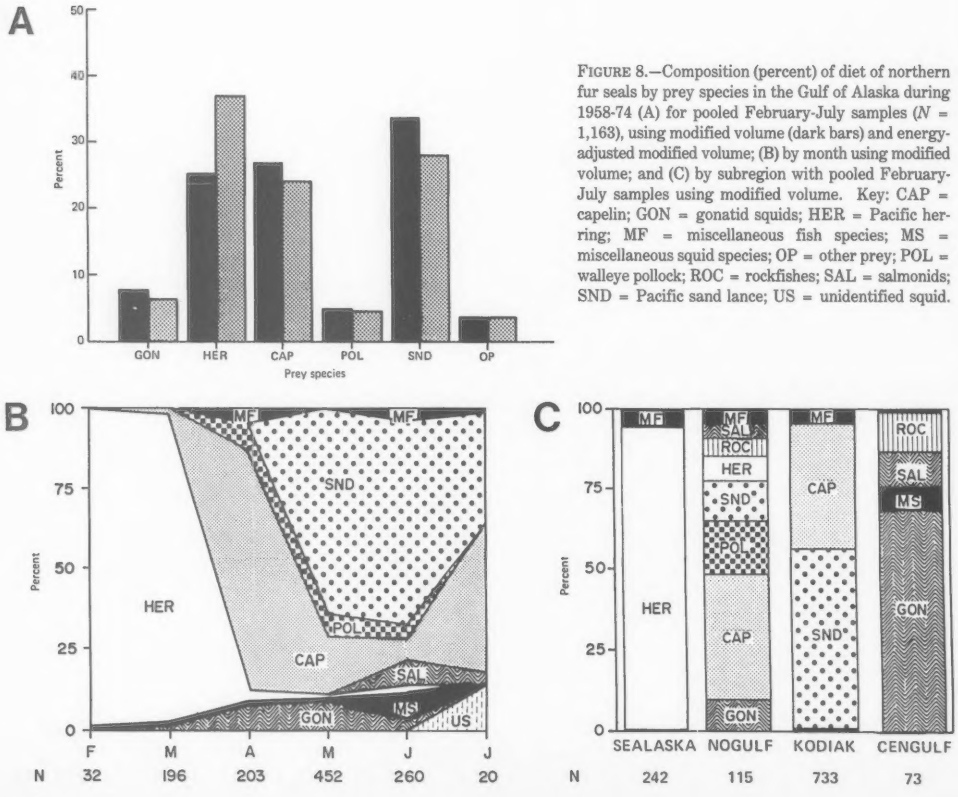

FIGURE 8.—Composition (percent) of diet of northern fur seals by prey species in the Gulf of Alaska during 1958-74 (A) for pooled February-July samples (N = 1,163), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled February-July samples using modified volume. Key: CAP = capelin; GON = gonatid squids; HER = Pacific herring; MF = miscellaneous fish species; MS = miscellaneous squid species; OP = other prey; POL = walleye pollock; ROC = rockfishes; SAL = salmonids; SND = Pacific sand lance; US = unidentified squid.

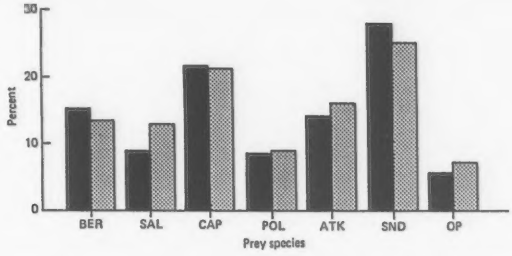

FIGURE 9.—Composition (percent) of diet of northern fur seals by prey species in western Alaska during 1958-74 for pooled May-October samples (N = 309), using modified volume (dark bars) and energy-adjusted modified volume. Key: ATK = Atka mackerel; BER = *Berryteuthis magister*; CAP = capelin; OP = other prey; POL = walleye pollock; SAL = salmonids; SND = Pacific sand lance.

Eastern North Pacific

Northern anchovy (20%) and Pacific herring (19%) were the main species eaten by the northern fur seals in the eastern North Pacific when data from all regions and months were pooled (Fig. 10). These prey were the most important whether energy content was considered or not, although importance increased when the caloric values were included. Salmonids (6%), capelin (8%), Pacific whiting (7%), walleye pollock (2%), Pacific sand lance (8%), and rockfishes (4%) were also commonly eaten. The remaining diet was made up of a wide variety of squids (mainly market squid, 6%; onychoteuthid squids, 6%; and gonatid squids, 5%) and other fishes (mainly Pacific saury, 4%; sablefish, 2%; and Atka mackerel, 2%). Squids were the primary food species in oceanic waters between California and the Gulf of Alaska, and fishes were the main prey in the neritic areas. Although not eaten in large amounts, salmonids and rockfishes were the main fishes consumed in oceanic areas between Washington and the Gulf of Alaska (Figs. 6C, 7C, 8C).

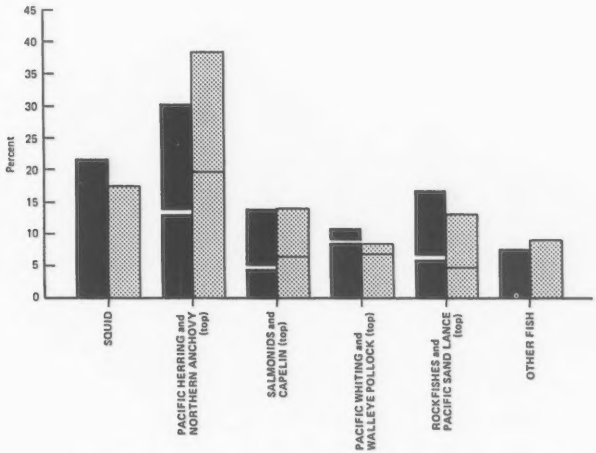

FIGURE 10.—Composition (percent) of diet of northern fur seals by prey species in the eastern North Pacific (excluding the Bering Sea) during 1958-74 using modified volume (dark bars) and energy-adjusted modified volume. Data from all months and years were pooled (N = 5,624).

Eastern Bering Sea

Walleye pollock was the most important food for northern fur seals in the eastern Bering Sea, particularly around the Pribilof Islands and in other inshore waters during July to September (Fig. 11A, B, C). Capelin was the main food near Unimak Pass during June to October. The squids, *Berryteuthis magister* and *Gonatopsis borealis*, were the primary prey species of fur seals in the oceanic areas (Fig. 11C). Deep-sea smelts (Bathylagidae) were eaten offshore, mainly in association with squid. The relative importance of each prey species was not markedly affected by the energy content adjustments (Fig. 11A).

Effect of Energy Value of Prey

In general, the ranking of prey species in the diet of northern fur seals was similar when using either modified volume or modified volume weighted for the energy content of prey. However, caloric values affected relative importance in regions where high energy foods (e.g., Pacific herring, northern anchovy, salmonids), or where low energy foods (e.g., market squid, Pacific whiting) were commonly eaten. In such cases, the adjustment shifted importance of a prey species in the same direction as the relative value of their caloric content compared with other prey in the diet. A species with high energy content increased in importance, but this caused others to decrease because the relative values of prey species in the diet all totaled 100%.

DISCUSSION

The results of earlier investigations on the diet of northern fur seals indicated that basically the

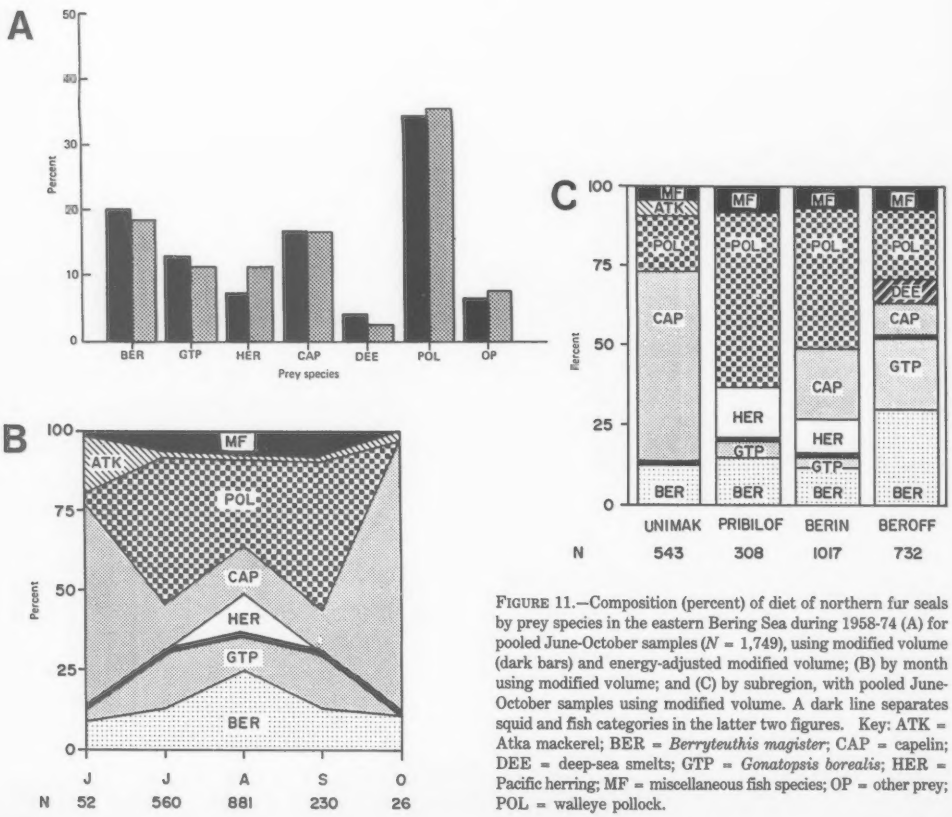

FIGURE 11.—Composition (percent) of diet of northern fur seals by prey species in the eastern Bering Sea during 1958-74 (A) for pooled June-October samples (N = 1,749), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion, with pooled June-October samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: ATK = Atka mackerel; BER = *Berryteuthis magister*; CAP = capelin; DEE = deep-sea smelts; GTP = *Gonatopsis borealis*; HER = Pacific herring; MF = miscellaneous fish species; OP = other prey; POL = walleye pollock.

same species of prey were important by region and month as reported in the current study. This was true for the numerous annual and intermittent summary reports prepared by the United States and Canada for the North Pacific Fur Seal Commission during 1958-74. However, they are not reviewed here because they typically described diet for a particular year or 2-6 yr period and were based on subsets of the samples that we used. In other studies, Stroud et al. (1981) and Kajimura (1984, 1985) mentioned, although did not demonstrate, that squids were the main food species in offshore areas, whereas fishes were the most important inshore. This observation was confirmed in our findings. The phenomenon appears to exist throughout the feeding range of northern fur seals off western North America.

Also, as found in our study, Taylor et al. (1955) and Kajimura (1985) reported that the main food for the northern fur seal off California was northern anchovy. Similarly, Clemens and Wilby (1933), Clemens et al. (1936), Schultz and Rafn (1936), May (1937), Wilke and Kenyon (1952), Spalding (1964), and Kajimura (1985) all indicated that Pacific herring was the primary prey between Washington and southeastern Alaska. Taylor et al. (1955) and Kajimura (1985) found that capelin was prominent in the diet off Kodiak Island; and Lucas (1899), Wilke and Kenyon (1952), and Kajimura (1985) found that walleye pollock was the most significant species in the eastern Bering Sea; and Wilke and Kenyon (1957) reported that capelin was important to northern fur seals near Unimak Pass.

However, there were some differences between the results of earlier research and the current analysis. Taylor et al. (1955) stated that 1) jacksmelt, *Atherinopsis californiensis*, was second in importance for northern fur seals off California rather than insignificant as we reported; 2) salmon was the main food off Oregon rather than a minor diet item; 3) walleye pollock was more important than Pacific herring off Washington; and 4) Pacific sand lance was rarely foraged off Kodiak Island rather than eaten almost as frequently as capelin. Kenyon (1956) found Pacific sandfish, *Trichodon trichodon*, to be the most commonly consumed food of seals which were taken on rookeries of the Pribilof Islands, whereas the current study found that it was rarely eaten. Most of these differences probably resulted from small sample sizes of earlier studies or dissimilar measures of importance. Also, some differences in diet will result from interannual variability in prey abundance and movement patterns owing to environmental conditions or other factors.

Factors other than just the relative importance by region and month must be taken into account when determining the significance of each prey species to the seal. Robbins (1983) stated that the nutritional value of food should also be considered. For example, food species with high caloric values will be more important than those with low caloric values because the amount of food required for metabolic functions depends to some extent upon the energy content of that food. However, high energy foods are more valuable only when they are not more difficult to capture and do not contain more indigestible or toxic substances than lower energy content species. These detrimental factors do not appear to be involved when considering the most important foods eaten by northern fur seals in the eastern North Pacific Ocean. Northern anchovy and Pacific herring were already the most important prey species even without accounting for their energy content. But because they also had relatively high energy values, their importance increased in the seal's diet. Thus, relative importance with an adjustment for energy content appears to be a better measure of diet than when energy content is not incorporated.

Another factor to consider is the proportion of the year that the northern fur seal population spends in each locality. Each prey species in the total annual diet should be weighted by the importance of each subregion and region where the prey is eaten. This weighting requires understanding the route and timing of migration, and the changes in local seasonal abundance of northern fur seals. The general pattern of migration for the Pribilof Islands stock is well known (Baker et al. 1970; Fiscus 1978; Bigg 1982[6]). Essentially all population components, except most 1-2 yr-olds, are thought to occur in the eastern Bering Sea during June-July to October where they pup, mate, nurse, and rest on the Pribilof Islands. Most 1-2 yr-olds remain in the North Pacific Ocean during this time. The stock leaves the eastern Bering Sea in November-December and travels mainly to the coastal areas between southeastern Alaska and California, with the largest number apparently going to California by January. Most males remain in Alaskan waters, and seals aged 1-2 yr remain offshore. The return migration starts in March-April with most seals arriving in the northern Gulf of Alaska by May. However, while this general pat-

[6]Bigg, M. A. 1982. Migration of northern fur seals in the eastern North Pacific and eastern Bering Sea: an analysis using effort and population composition data. Unpubl. rep., 77 p. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada.

tern of migration is known, no estimates have been made of the seasonal abundance of seals by region, and thus total diet cannot be weighted by the significance of each locality.

Nonetheless, we are of the opinion that the lack of estimates of local abundance of northern fur seals may not be a major bias in our descriptions of diet for the large coastal regions of the eastern North Pacific (Fig. 10) and the eastern Bering Sea (Fig. 11). We reason that the sampling effort in the eastern North Pacific was extensive from December to June, as indicated by the size of samples collected by month and region (Figs. 4-9; see also Figure 2), and may have largely reflected the seasonal changes in relative abundance of seals during their coastal migration. For the eastern Bering Sea, essentially all samples were taken during July-October, which was the time most seals resided there.

The most general conclusion to be made about the diet of coastal northern fur seals is that it consists primarily of small schooling fish. Previous studies have made the point that the diet consists of small schooling fish and squid (Spalding 1964; Kajimura 1985; others). However, our findings suggest that squid are no more important in the overall diet to the seal than are the larger sized fish. In the coastal regions of the eastern North Pacific the northern fur seal's diet consists of 60% small schooling fish, 23% other fish, and 17% squid. When northern fur seals arrive off the coast of southeastern Alaska to California during winter, they feed on northern anchovy, Pacific herring, capelin, and Pacific saury. When most northern fur seals arrive along the coast of the Gulf of Alaska in spring, they eat capelin and Pacific sand lance. These are fish <30 cm in length (Table 2). Typically they are eaten whole whereas larger fish are first broken into small pieces (Spalding 1964). Walleye pollock is the primary food in the eastern Bering Sea. It is a large fish as an adult (Smith 1981), and these fish school. However, northern fur seals feed mainly upon the juvenile stages, i.e., <20 cm (McAlister and Perez[7]). Thus, the diet in this region consists up to 64% small schooling fish, 6% other fish, and 30% squid.

On the Asian coast the diet of northern fur seals also includes small schooling fishes such as myctophiform fishes (lanternfishes), Pacific saury, Pacific sand lance, and the Japanese anchovy, *Engraulis japonicus*, in addition to walleye pollock and squid (Taylor et al. 1955; Lander and Kajimura 1980). Of interest is the fact that in recent years the Japanese sardine, *Sardinops melanosticta*, has become more important in the diet of northern fur seals off Asia (Yoshida et al.[8,9]; Yoshida and Baba[10,11]). This sardine was depleted during the 1930's and 1940's and

TABLE 2.—Summary of the size range and general habitat of northern fur seal prey.[1] A = anadromous; BC = British Columbia; BER = eastern Bering Sea; CAL = California; GULF = Gulf of Alaska; I = inshore; NS = near surface; O = offshore; ORE = Oregon; S = schooling fish; WASH = Washington; WEST = western Alaska.

Prey	Average adult size (cm)	Size range (cm) of specimens in fur seal stomachs (sample size in parentheses)[2]	General habitat
Pacific herring	<20-30	10-25 (11,>27)	Pelagic (I,S)
Northern anchovy	<18	9-18 (7,27)	Pelagic (I-O,S)
Salmonids[3]	<80	15-41 (22,>26)	Pelagic (I-O,A)
Capelin	22	7-14 (7,64)	Pelagic (I,S)
Eulachon	23-30	12-21 (3,11)	Pelagic (I,S,A)
Deep-sea smelts	2-18	8-12 (6,986)	Pelagic (O,S)
Myctophiform fishes	13-20	—	Pelagic (O,S)
Pacific saury	10-32	25 (1,4)	Pelagic (O,S)
Pacific whiting	66-76	15 (1,2)	Pelagic and semidemersal (I-O,S)
Walleye pollock	<90	4-40 (71,1721)	Pelagic and semidemersal (I-O,S)
Rockfishes	30-53	11-31 (6,>19)	Demersal (I-O,S)
Sablefish	57-60	20-31 (3,>3)	Pelagic and semidemersal (I-O,S)
Atka mackerel	<120	15-23 (5,>5)	Pelagic and semidemersal (I,S)
Pacific sand lance	20	—	Demersal (I,S)
Market squid	14-17	7-15 (6,43)	Pelagic (I)
Onychoteuthid squids[4]	10-37	14-22 (3,>3)	Pelagic (I-O)
Gonatid squid	12-32	5-24 (10,>59)	Pelagic (I-O)

[1]Data on average lengths of prey and ecology were compiled from Akimushkin (1963), Bakkala et al. (1981), Baxter (1967), Baxter and Duffy (1974), Carl (1964), Childress and Nygaard (1973), Childress et al. (1980), Fields (1965), Fitch (1974), Fitch and Lavenberg (1968, 1971, 1975), Hart (1973), Inada (1981), Miller and Lea (1976), Naito et al. (1977), Niggol (1982), Pearcy (1965), Pearcy et al. (1979), Smith (1981), Taka et al. (1980), and Wespestad and Barton (1981).

[2]Total length for fish and dorsal mantle length for squid. The first number in parentheses is the number of fur seal stomachs examined, and the second number in parentheses is the number of prey specimens measured. These data were derived from an analysis of the original unpublished 1958-74 data.

[3]Maximum size of salmonids found at sea. Adults in freshwater are larger (to 147 cm) depending upon species.

[4]Does not include size range of *Moroteuthis* (<140 cm) which has been taken by northern fur seals, but rarely off North America.

[7]McAlister, W. B., and M. A. Perez. 1977. Ecosystem dynamics—birds and marine mammals. Part 1: preliminary estimates of pinniped-finfish relationships in the Bering Sea (final report). *In* Environmental assessment of the Alaskan continental shelf, Annual Report 12, p. 342-371. U.S. Department of Commerce, Environmental Research Laboratory, Boulder, CO.

[8]Yoshida, K., N. Okumoto, and N. Baba. 1979. Japanese pelagic investigation on fur seals, 1978. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-9, 66 p.

recovered only recently (Kondo 1980). The northern fur seal appears to have reacted to this recovery by eating more sardines. A similar change in diet may have taken place off California during the past 50 years. The Pacific sardine, *Sardinops sagax*, was once the most abundant small, schooling fish off California, whereas now northern anchovy is (Murphy 1966; Smith 1972; Mais 1974). The Pacific sardine population was drastically reduced during the 1940's mainly because of fishing pressure and has remained at a relatively low level since, while the northern anchovy increased in abundance during the 1950's and the 1960's (Vrooman and Smith 1971; Hart 1973; Wolf and Smith 1985). The Pacific sardine may undergo long-term periodic fluctuations in population size (Thompson 1921), and it may now once again be increasing in biomass (Wolf and Smith 1985). Northern fur seals have not eaten Pacific sardine in recent years, but perhaps they fed on this species prior to the 1940's. The seal may have changed its diet from largely Pacific sardine to northern anchovy. Unfortunately, the stomach contents of only two northern fur seals were collected from California prior to the 1950's (Scheffer 1950). Clemens and Wilby (1933) gave the only evidence that sardines were once consumed by these seals in the eastern North Pacific Ocean. They found that sardines were commonly eaten during 1931 off southwestern Vancouver Island.

An interesting speculation regarding the significance of small schooling fish to northern fur seals is the relationship between diet and the migration route of the seal. Small schooling fish could be important just because they are abundant and lie along the coastal migration path of northern fur seals. Kajimura (1985) argued for this possibility. He suggested that the migration pattern of northern fur seals is genetically established and that the seal feeds opportunistically upon whatever prey species are most abundant in its path. He believes that, although food is not a major factor in determing the migration route of northern fur seals, the movements of prey species can still alter the local distribution of fur seals. An alternative possibility is that the seals learn the location of the main foods and then selects its migration route to include them. Baker (1978) argued for this alternative. He proposed that, while some inherited factors may be involved in migration, northern fur seals could mainly search the North Pacific Ocean for the most preferred or abundant food, and thereafter establish the migration route. Such being the case, perhaps inexperience explains why 1-2 yr-old seals are rarely seen inshore feeding with older seals. Also, perhaps squid is not a preferred or sufficiently available food for northern fur seals offshore, because most seals older than 1-2 yr feed inshore on fish. However, at this stage, not enough is known about the factors that control migration of the northern fur seal to establish which alternative is true. As Kajimura (1985) has pointed out, factors other than diet are no doubt involved as indicated by the fact that males do not migrate as far south as females.

[9]Yoshida, K., N. Okumoto, and N. Baba. 1981. Japanese pelagic investigation on fur seals, 1979-1980. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-10, 150 p.

[10]Yoshida, K., and N. Baba. 1983. Japanese pelagic investigation on fur seals, 1981-1982. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-11, 118 p.

[11]Yoshida, K., and N. Baba. 1984. Japanese pelagic investigation on fur seals, 1983. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-12, 67 p.

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LITERATURE CITED

AKIMUSHKIN, I. I.
1963. Cephalopods of the seas of the U.S.S.R. [In Russ.] Izd. Akad. Nauk, Mosc. (Transl. by Isr. Prog. Sci. Transl., 1965, avail. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT65-50013, 223 p.)

BAKER, R. C., F. WILKE, AND C. H. BALTZO.
1970. The northern fur seal. U.S. Fish Wildl. Serv., Circ. 336, 20 p.

BAKER, R. R.
1978. The evolutionary ecology of animal migration. Holmes and Meier Publ., N.Y., 1012 p.

BAKKALA, R., K. KING, AND W. HIRSCHBERGER.
1981. Commercial use and management of demersal fish. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: Oceanography and resources, vol. 2, p. 1015-1036. Univ. Wash. Press, Seattle, WA.

BAXTER, J. L.
1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 11:110-116.

BAXTER, J. L., AND J. M. DUFFY.
1974. Inshore fishes of California, 4th revision. Calif. Dep. Fish Game, Sacramento, CA, 78 p.

BIGG, M. A., AND I. FAWCETT.
1985. Two biases in diet determination of northern fur seals

(*Callorhinus ursinus*). *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (editors), Marine mammals and fisheries, p. 284-291. George Allen & Unwin (Publ.), Lond.

BIGG, M. A., I. B. MACASKIE, AND G. ELLIS.
1978. Studies on captive fur seals. Progress Rep. No. 2. Can. Fish. Mar. Serv. Manuscr. Rep. 1471, 21 p. Nanaimo, B.C.

BIGG, M. A., AND M. A. PEREZ.
1985. Modified volume: a frequency-volume method to assess marine mammal food habits. *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (editors), Marine mammals and fisheries, p. 277-283. George Allen & Unwin (Publ.), Lond.

CARL, G. C.
1964. Some common marine fishes of British Columbia. B.C. Prov. Mus., Victoria, B.C., Handb. No. 23, 86 p.

CHILDRESS, J. J., AND M. H. NYGAARD.
1973. The chemical composition of midwater fishes as a function of depth of occurrence off southern California. Deep-Sea Res. 20:1093-1109.

CHILDRESS, J. J., S. M. TAYLOR, G. M. CAILLIET, AND M. H. PRICE.
1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off southern California. Mar. Biol. 61:27-40.

CLEMENS, W. A., J. L. HART, AND G. V. WILBY.
1936. Analysis of stomach contents of fur seals taken off the west coast of Vancouver Island in April and May 1935. Can. Dep. Fish., Ottawa, 20 p.

CLEMENS, W. A., AND G. V. WILBY.
1933. Food of the fur seal off the coast of British Columbia. J. Mammal. 14:43-46.

FIELDS, W. G.
1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish Bull. 131, 108 p.

FISCUS, C. H.
1978. Northern fur seal. *In* D. Haley (editor), Marine mammals of eastern North Pacific and arctic waters, p. 152-159. Pac. Search Press, Seattle, WA.

FITCH, J. E.
1974. Offshore fishes of California. 5th rev. Calif. Dep. Fish Game, Sacramento, CA, 80 p.

FITCH, J. E., AND R. J. LAVENBERG.
1968. Deep-water teleostean fishes of California. Univ. Calif. Press, Berkeley, CA, 155 p.
1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, CA, 179 p.
1975. Tidepool and nearshore fishes of California. Univ. Calif. Press, Berkeley, CA, 156 p.

HART, J. L.
1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180, 740 p.

INADA, T.
1981. Studies on the Merlucciid fishes. Bull. Far Seas Fish. Res. Lab. (Shimizu) 18:1-172.

KAJIMURA, H.
1984. Opportunistic feeding of the northern fur seal *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-779, 49 p.
1985. Opportunistic feeding by the northern fur seal, (*Callorhinus ursinus*). *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (editors), Marine mammals and fisheries, p. 300-318. George Allen & Unwin (Publ.), Lond.

KENYON, K. W.
1956. Food of fur seals taken on St. Paul Island, Alaska, 1954. J. Wildl. Manage. 20:214-215.

KIZEVETTER, I. V.
1971. Chemistry and technology of Pacific fish. Dal'izdat, Vladivostok. (Transl. by Isr. Prog. Sci. Transl., 1973, avail. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT72-50019, 304 p.)

KONDO, K.
1980. The recovery of the Japanese sardine - the biological basis of stock-size fluctuations. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177:332-354.

LANDER, R. H. (editor).
1980. Summary of northern fur seal data and collection procedures. Vol. 2: Eastern Pacific pelagic data of the United States and Canada (excluding fur seals sighted). U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-4, 541 p.

LANDER, R. H., AND H. KAJIMURA (editors).
1980. Summary of northern fur seal data and collection procedures. Vol. 3: Western Pacific pelagic data of the Soviet Union and Japan, 1958-1978 (excluding fur seals sighted). U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-5, 304 p.

LUCAS, F. A.
1899. The food of the northern fur seals. *In* D. S. Jordan et al. (editors), The fur seals and fur-seal islands of the North Pacific Ocean, Part 3, p. 59-68. Gov. Print. Off., Wash., DC.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.

MAY, F. H.
1937. The food of the fur seal. J. Mammal. 18:99-100.

MILLER, D. J., AND R. N. LEA.
1976. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 249 p. [1972, addendum added 1976.]

MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. (4th Ser.) 34:1-84.

NAITO, M., K. MURAKAMI, AND T. KOBAYASHI.
1977. Growth and food habit of oceanic squids (*Ommastrephes bartrami*, *Onychoteuthis borealijaponicus*, *Berryteuthis magister* and *Gonatopsis borealis*) in the western subarctic Pacific region. [In Jpn., Engl. summ.] *In* Fisheries biological production in the subarctic Pacific region, p. 339-351. Res. Inst. North Pac. Fish. Fac. Fish., Hokkaido Univ., Spec. Vol. 1977.

NIGGOL, K.
1982. Data on fish species from Bering Sea and Gulf of Alaska. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-29, 125 p.

PEARCY, W. G.
1965. Species composition and distribution of pelagic cephalopods from the Pacific Ocean off Oregon. Pac. Sci. 19:261-266.

PEARCY, W. G., T. NEMOTO, AND M. OKIYAMA.
1979. Mesopelagic fishes of the Bering Sea and adjacent northern North Pacific Ocean. J. Oceanogr. Soc. Jpn. 35: 127-134.

ROBBINS, C. T.
1983. Wildlife feeding and nutrition. Acad. Press, N.Y., 343 p.

SCHEFFER, V. B.
1950. The food of the Alaska fur seal. U.S. Fish Wildl. Serv., Bur. Commer. Fish., Wildl. Leafl. 329, 16 p.

SCHULTZ, L. P., AND A. M. RAFN.
1936. Stomach contents of fur seals taken off the coast of Washington. J. Mammal. 17:13-15.

SIDWELL, V. D.
1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks, and their products. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/SEC-11, 432 p.

SIDWELL, V. D., P. R. FONCANNON, N. S. MOORE, AND J. C. BONNET.
1974. Composition of the edible portion of raw (fresh or frozen) crustaceans, finfish and mollusks. I. Protein, fat, moisture, ash, carbohydrate, energy value, and cholesterol. Mar. Fish. Rev. 36(3):21-35.

SMITH, G. B.
[1981.]. The biology of walleye pollock. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: Oceanography and resources, Vol. 1, p. 527-551. U.S. Gov. Print. Off., Wash., DC.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. U.S. Natl. Mar. Fish. Serv., Fish. Bull. 70:849-874.

SPALDING, D. J.
1964. Comparative feeding habits of the fur seal, sea lion, and habour seal on the British Columbia coast. Bull. Fish. Res. Board Can. 146, 52 p.

STANSBY, M. E.
1976. Chemical characteristics of fish caught in the northeast Pacific Ocean. Mar. Fish. Rev. 38(9):1-11.

STROUD, R. K., C. H. FISCUS, AND H. KAJIMURA.
1981. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington. U.S. Natl. Mar. Fish. Serv., Fish. Bull. 78: 951-959.

TAKA, S., M. KITAKATA, AND T. WADA.
1980. Food organisms of saury, *Cololabis saira* (Brevoort) and vertical distribution of zooplankton in the southeast waters off Kuril Islands in July, 1976-1978. [In Jpn., Engl. summ.] Bull. Hokkaido Reg. Fish. Res. Lab. 45:15-41.

TAYLOR, F. H. C., M. FUJINAGA, AND F. WILKE.
1955. Distribution and food habits of the fur seals of the North Pacific Ocean. U.S. Dep. Inter., Fish Wildl. Serv., Wash., DC, 86 p.

THOMPSON, W. F.
1921. The future of the sardine. Calif. Fish Game 7:38-41.

VROOMAN, A. M., AND P. E. SMITH.
1971. Biomass of the subpopulations of northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 15:49-51.

WATT, B. K., AND A. L. MERRILL.
1963. Composition of foods...raw, processed, prepared. U.S. Dep. Agric., Agric. Handb. 8, 190 p.

WESPESTAD, V. G., AND L. H. BARTON.
[1981]. Distribution, migration, and status of Pacific herring. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: Oceanography and resources, Vol. 1, p. 509-525. U.S. Gov. Print. Off., Wash., DC.

WILKE, F., AND K. W. KENYON.
1952. Notes on the food of fur seal, sea lion and harbor porpoise. J. Wildl. Manage. 16:396-397.
1954. Migration and food of the northern fur seal. Trans. North Am. Wildl. Nat. Resour. Conf. 19:430-440.
1957. The food of fur seals in the eastern Bering Sea. J. Wildl. Manage. 21:237-238.

WOLF, P., AND P. E. SMITH.
1985. An inverse egg production method for determining the relative magnitude of Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 26:130-138.

WOOTTON, R. J.
1976. The biology of the sticklebacks. Acad. Press, Lond., 387 p.

INSTAR IDENTIFICATION AND LIFE HISTORY ASPECTS OF JUVENILE DEEPWATER SPIDER CRABS, *CHIONOECETES TANNERI* RATHBUN

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ABSTRACT

For the deepwater spider crab, *Chionoecetes tanneri*, seven instars from first crab stage (3.8 mm carapace width (CW)) to instar VII (26.8 mm CW) are identified from size-frequency histograms. The average growth per molt for the first seven instars is 39% and the time from egg to instar VII is estimated to be 20 months.

Measurements of chela length, abdomen width and carapace width were used to define two growth phases for *C. tanneri* and to determine size at maturity for males (142.7 mm CW) and females (102.3 mm CW). The unequal sex ratio of adults (29% males) and presence of chitinoclastic lesions on 76% of the adult females as compared with only 29% of the adult males suggest that adult females are anecdysic.

In this study of material collected off the southern Oregon coast, the mean adult carapace widths for males and females is very close to the sizes reported for adult males and females (148.9 and 102.5 mm CW respectively) from the northern Oregon coast. The similarity in size extends to the material collected from near the type location (Gulf of the Farallons) where instars VI and VII are 19.4 and 27.3 mm CW compared with 19.8 and 26.7 mm CW for the same instars from the southern Oregon coast. The biotic stability at depths of maximum abundance (500-775 m) contributes to this uniformity.

The spider (or tanner) crab, *Chionoecetes tanneri* Rathbun, is similar in size and morphology to the better known and commercially harvested species *C. bairdi* and *C. opilio*. Unlike *C. bairdi* and *C. opilio* which are typically encountered in shallow waters and are not reported deeper than 400 m in the eastern Pacific, *C. tanneri* is a deep-water species which ranges to 1,925 m and has its maximum abundance at 500-775 m (Pereyra 1972).

Although *C. tanneri* is not likely to be fished commercially because of its deep-water habitat and certain aspects of its biology, Somerton (1981) suggested that fluctuating supplies of Alaskan crab species might promote more economical methods for fishing in deep water. Red crab, *Geryon quinquedens*, taken from depths of 257-1,000 m between Georges Bank and Cape Hatteras are landed commercially in limited numbers on the eastern seaboard (Lux et al. 1982; U.S. National Marine Fisheries Service Fisheries Statistics 1985).

In part, because of its deep-water habitat, certain life history aspects of *C. tanneri* are not well known. Pereyra (1966, 1968) determined size at maturity and described the seasonal distribution of adult and late juvenile crabs. Egg development follows a yearly cycle with release of matured eggs and ovulation of new eggs during the winter (Pereyra 1966). After hatching, the total larval (pelagic) phase (prezoea, zoea I, II and megalopa) is estimated to be 80 d (Lough 1974). Samples collected mainly from a series of cruises off the Oregon coast from 1972 to 1975 have provided us with *C. tanneri* specimens from the first crab stage to adult. These specimens have made it possible to identify a series of early instars and to determine juvenile growth rates; they also provided life history information on size at maturity and adult and juvenile sex ratios for comparison with earlier work. In addition, observations of the carapace condition of adults helped to substantiate the anecdysic condition of adult females.

METHODS

Sampling

Samples of *C. tanneri* were collected off the continental shelf and slope areas adjacent to Coos Bay, OR (lat. 42°25′N, long. 124°50′W) in depths ranging from 300 to 1,200 m during 10 cruises between April 1973 and March 1975. A total of 1,625 crabs

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of both sexes ranging in size from 10 to 165 mm carapace width (CW) were captured using two types of trawl gear: a 9 m semi-baloon Gulf of Mexico shrimp trawl and a 3 m beam trawl (Carey and Heyamoto 1972). The stretched dimension of the mesh for both trawl nets was 38 mm (1.5-in), and the cod ends were lined with 12.7 mm (0.5-in) mesh. In addition 47 of the smallest crabs (3-10 mm CW) were found in the gut contents of sable fish, *Anoplopoma fimbria*, and Dover sole, *Microstomus pacificus*, caught in these trawls. The Smithsonian Institution provided another 306 juvenile tanner crabs taken near the type location for *C. tanneri* west of the Farallon Islands (lat. 37°30'N, long. 122°59'W) (Rathbun 1925) at 500-783 m.

Size at Maturity

The size at maturity for both male and female *C. tanneri* was based on allometric measurements. Allometry compares the difference in the proportions of specific body parts with changes in absolute size of a major body axis (Gould 1966). In Brachyura the allometric growth of secondary sex characters is well documented (Tessier 1960; Hartnoll 1969). In the genus *Chionoecetes* it takes the form of differential enlargement of the abdomen and modification of pleopods in females whereas the size and shape of the chelae are modified in the males (Watson 1970; Brown and Powell 1972).

Carapace width for both male and female crabs was measured at its widest part (mesobranchial region) exclusive of spines (Fig. 1A). The male carapace width was compared with the length of the chelar propodus (CPL) which is measured from the joint between the carpus to the tip of the fixed finger of the propodus (Fig. 1B), whereas the female carapace width was compared with the width of the abdomen (AW) which is measured at its widest part (fifth segment) (Fig. 1C). Males with worn or broken chelipeds were not used. All measurements were made to the nearest 0.01 mm using precision dial calipers, and numbers were rounded to the first decimal for plotting. Plots of the measurements of CW vs. CPL and CW vs. AW were used to identify size at maturity for males and females.

Size-Frequency Histograms, Growth, and Sex Ratio

Measurements of the carapace width were taken from the 1,978 crabs available. Size-frequency histograms were constructed and seven juvenile instars were identified from dominant modes. Adult *C. tanneri* are sexually dimorphic with respect to body size (Pereyra 1972). Since we did not know at which molt this size dimorphism was first evident, the data for males and females was shaded differently in the size-frequency histogram. The juvenile sex ratio was

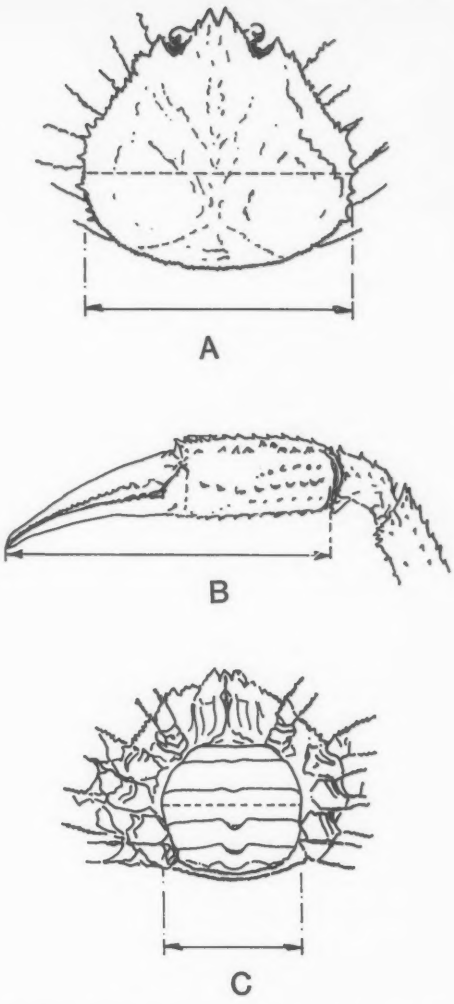

FIGURE 1.—Body dimensions of *Chionoecetes tanneri* measured for size-frequency and allometric analyses. (A) Carapace width (♂ and ♀) measured at its widest part across the mesobranchial region and exclusive of spines. (B) Chelar propodus length (♂) measured from the joint between the carpus and the tip of the fixed finger of the propodus. (C) Abdomen width (♀) measured at its widest part, across the fifth segment.

calculated for each instar, and when it was clear from the equal sex ratio that juvenile males and females were not dimorphic, the percent increase in carapace width per molt was computed as

$$\text{Percent increase in CW (mm)} = \frac{\text{Postmolt CW (mm)} - \text{Premolt CW (mm)}}{\text{Premolt CW (mm)}} \times 100$$

In one series of size-frequency histograms from samples collected in June, July, and August 1974 and January and March 1975, the progression of modes (representative of instars of the small juveniles from fish gut contents) was used to estimate growth rate. The next larger instar (CW = 10 mm) was the first to be consistently sampled by the trawl gear. Starting with the 10 mm CW instar from April 1973, growth of juvenile tanner crabs was followed through August, October, and November 1973 and March 1974.

Carapace Condition

Detailed observations were made of the carapace on each specimen and included hardness, amount of attached fauna, and general condition. Darkened and softened or weakened areas on the carapaces were similar to those caused by chitinoclastic bacteria (Sindermann 1970) and were thought to be associated with age. Adult female *C. tanneri* were especially subject to carapace deterioration.

RESULTS AND DISCUSSION

Since a high degree of correlation between gonad maturity and external morphology has been shown for the genus *Chionoecetes* (Brown and Powell 1972; Donaldson et al. 1981), a plot of carapace width and chela length (Fig. 2) was used to define adult males. Specimens with chelae longer than 85 mm (corresponding to carapace width >118 mm) were assumed to be sexually mature males. Those females

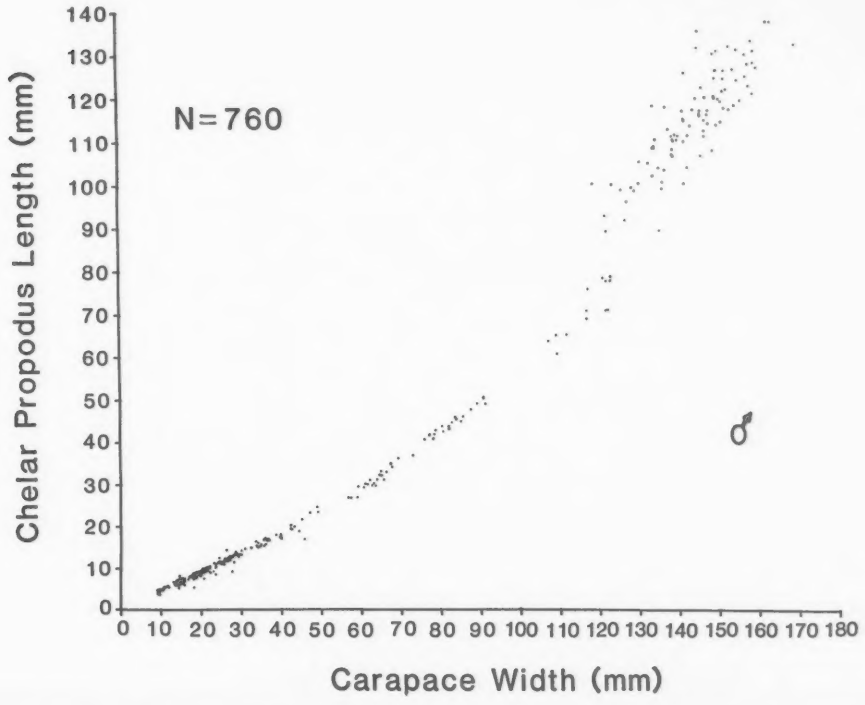

FIGURE 2.—Relationship between carapace width and chelar propodus length for juvenile and adult male *Chionoecetes tanneri*.

with abdomen widths > 50 mm (corresponding to carapace widths >85 mm) form a well-defined group (Fig. 3) of adults. The mean carapace width for adult male and female crabs in this study was 142.7 and 102.3 mm respectively and was compared with the mean carapace widths of 148.9 and 102.5 mm for females given by Pereyra (1972) for adult *C. tanneri* collected south of the Columbia River mouth. Brown and Powell (1972) reported a similar correspondence in adult carapace widths for *C. bairdi* collected from locations in Alaska. The large variation in size of mature male *C. bairdi* in the eastern Bering Sea was clearly related at the clinal variation temperature (Somerton 1981).

Seven modes representing juvenile instars are evident from the size-frequency histograms (Fig. 4). The mean carapace widths for each juvenile instar were calculated and subsequently the increase in CW per molt was computed (Table 1). The average increase at each molt for instars I-VII is 39% and there is no difference in growth increment of juvenile males and females In a laboratory study using *C. opilio*, Miller and Watson (1976) reported that growth per molt for immature females was significantly greater than for immature males. But the findings of Hilsinger et al. (1975) agree with ours. They found no difference in growth rate for juvenile male and female *C. bairdi* and reported a constant growth rate of 27% for juvenile females. The change in the slope of the regression lines of the log-log plots of the allometric measurements of *C. tanneri* (Fig. 5) indicated a change in the rate of growth only at sexual maturity. *Chionoecetes tanneri*, like *C. opilio* (Watson 1970), showed two growth phases, one for juveniles and one for adults.

If *C. tanneri* eggs hatch predominantly in winter (January-March) and the total larval life is 80 d, the recruitment of the smallest crab stage (CW = 4) to the population in June-July is in agreement with our findings. Instars can be followed from 4 mm CW (instar I) in June and July 1974, to 5.5 cm CW (instar II) in August 1974, to 7.5 mm CW (instar III) in January 1975 (Fig. 6). The smallest specimens sampled by the trawls were about 10 mm CW, and there were relatively large numbers of these instar IV specimens in April 1973 which molted to instar V by August and to instar VI in October 1973 (Fig. 7). No growth of these instar VI crabs is evident from the November 1973 or March 1974 data. We estimate approximately 20 mo from egg hatching to instar VII (CW = 26.8 mm) (Fig. 8).

Observations on general carapace condition and abundance of epifauna indicate that adult male *C. tanneri* do molt frequently enough to maintain their

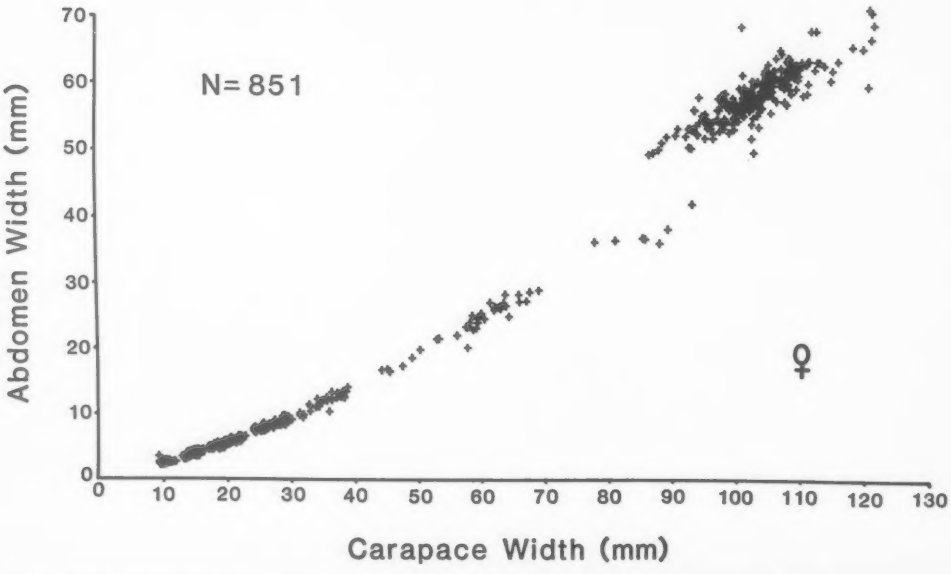

FIGURE 3.—Relationship between carapace width and abdomen width for juvenile and adult female *Chionoecetes tanneri*.

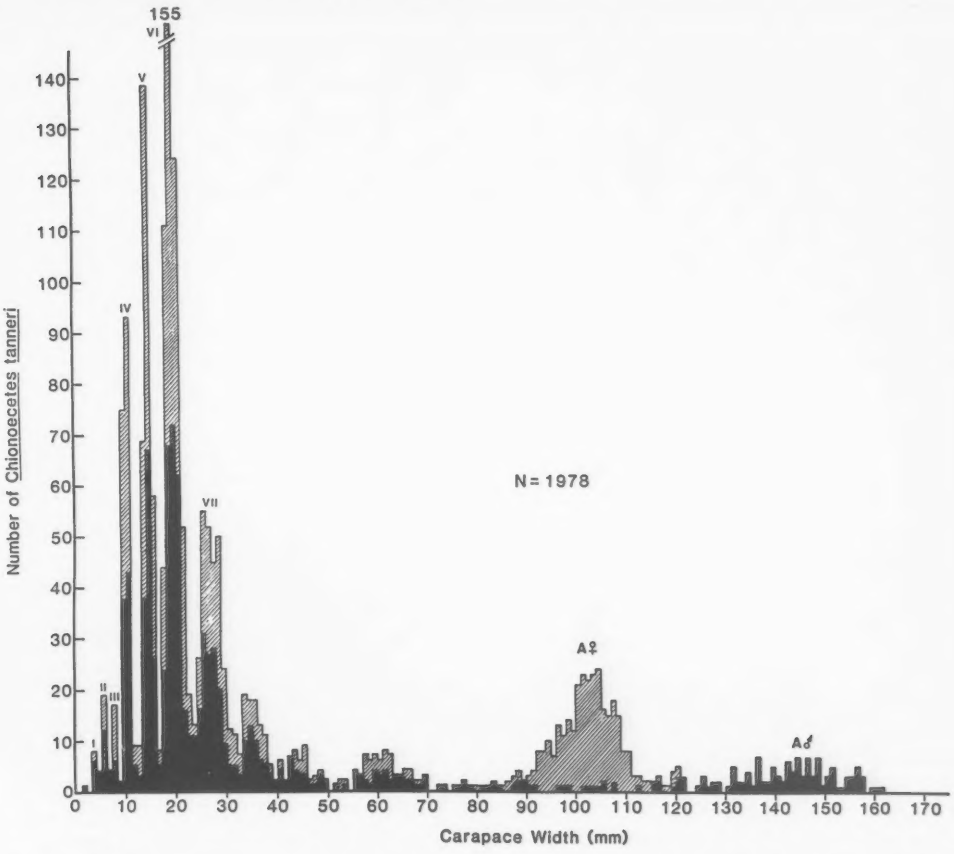

FIGURE 4.—Size-frequency histograms representing all specimens of *Chionoecetes tanneri* collected off the Oregon coast 1973-75 and from the Gulf of the Farallons. Instars I-VII are indicated. Males are shown in solid color.

carapaces relatively free of epifauna and lesions caused by bacterial infections (Baross et al. 1978). Of the 290 adult female specimens examined, 87% showed exoskeleton lesions and these adult females also had the highest diversity and abundance of epifauna on their exoskeletons. Only 29% of the 124 adult males observed showed the effect of chitinoclastic bacterial infection. No lesions or epifauna were found on any of the 1,447 juveniles examined. In contrast to the findings of Hartnoll (1969) who worked with shallow-water spider crabs, observations of the carapace condition of adult male and female *C. tanneri* suggests adult males continue to molt after maturity while adult females are anecdysic, a finding consistent with Watson's (1970) data for *C. opilio*. The unequal adult sex ratio (29% males, Table 1) is also an indication that males may be subjected to the differential mortality of continued molting.

The agreement of mean CW for adults collected off the Oregon coast in the study and that of Pereyra's (1966) work has an interesting corollary in the material collected from near the Farallon Islands. The mean carapace width of instars VI and VII for *C. tanneri* collected west of the Farallon Islands is 19.4 and 27.3 mm respectively. The carapace widths for the same instars collected from Oregon is 19.8 and 26.7 mm. Childress and Price (1978) credited the constant increase in size between each pair of instars in the deep-living, midwater

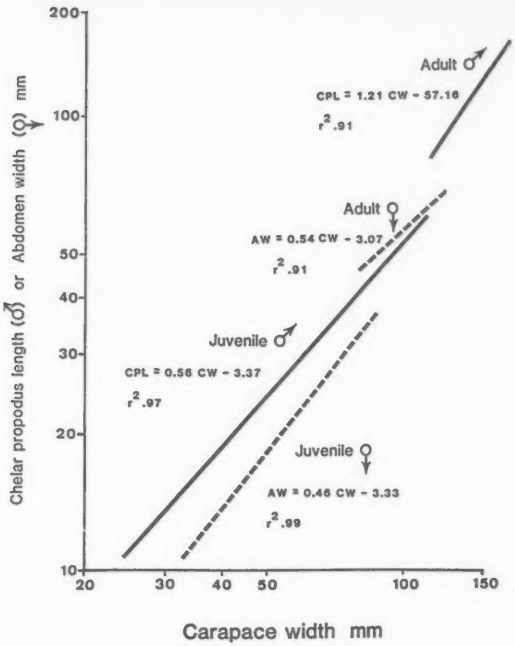

FIGURE 5.—Growth phases for juvenile and adult *Chionoecetes tanneri*. CPL = Chelar propodus length (mm); CW = Carapace width (mm); AW = Abdomen width (mm).

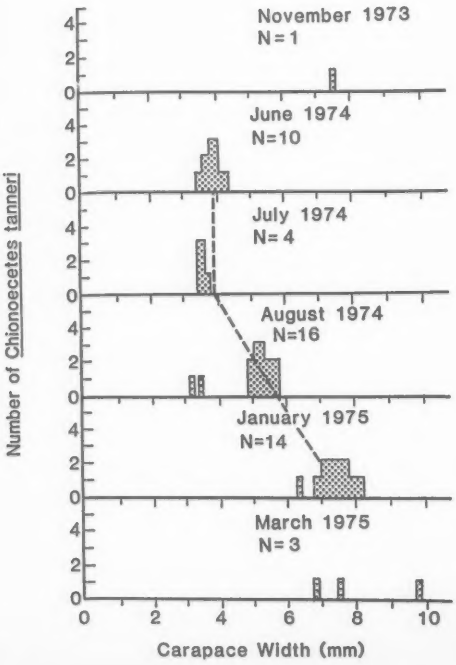

TABLE 1.—Percent increase in mean carapace width and sex ratio (males %) for successive instars of *Chionoecetes tanneri*.

Instar	*N*	Males (%)	Carapace width (mm) Mean	Carapace width (mm) s^2	Increase in carapace width (%)
I	16	53	3.80	0.25	
					48.4
II	19	—	5.64	0.62	
					35.8
III	18	53	7.66	0.53	
					31.7
IV	175	49	10.09	0.57	
					43.0
V	281	49	14.43	0.68	
					36.5
VI	499	50	19.69	1.18	
					36.6
VII	268	53	26.83	3.40	
—					
—					
Adults	411	29			

FIGURE 6.—Size-frequency histograms representing early juveniles with carapace widths < 9 mm. These samples were collected from stomachs of benthic fish. The dashed line represents the progression of instars through time with first crab stage in June to instar II in August and instar III in January.

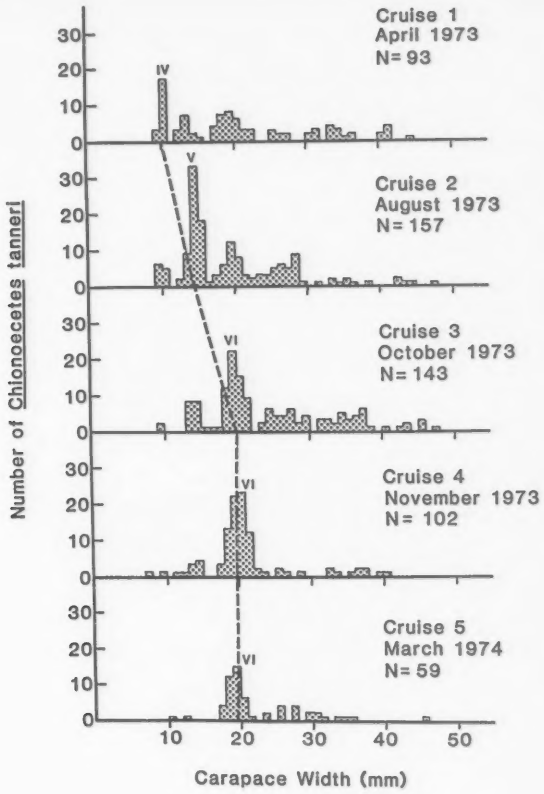

FIGURE 7.—Size-frequency histograms representing juveniles with carapace widths 10-50 mm wide. The dashed line represents progression of instars through time with instar IV in April, instar V in August and instar VI in October through March.

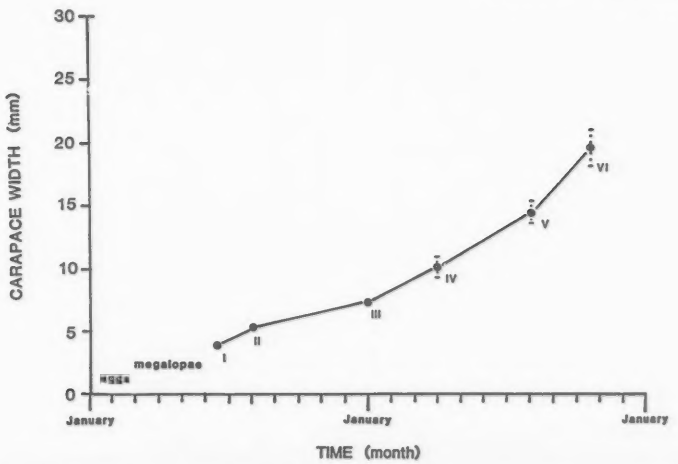

FIGURE 8.—Growth rate of *Chionoecetes tanneri* from egg to seventh instar is estimated to be at least 20 mo. Dotted lines indicate standard deviation.

mysid, *Gnathophausis ingens*, to the physical and biotic stability of this species' environment. Various environmental factors can alter both the dimensions and the number of molts in many species of crustaceans. At depths of maximum abundance (500-775 m) of *C. tanneri*, the annual water ranges from 2.3° to 5.6°C and certainly this uniform environment contributes to the consistency of instar size and size at maturity.

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LITERATURE CITED

BAROSS, J. A., P. A. TESTER, AND R. Y. MORITA.
1978. Incidence, microscopy, and etiology of exoskeleton lesions in the tanner crab, *Chionoecetes tanneri*. J. Fish. Res. Board Can. 35:1141-1149.

BROWN, R. B., AND G. C. POWELL.
1972. Size at maturity in the male Alaskan tanner crab, *Chionoecetes bairdi*, as determined by chela allometry, reproductive tract weights, and size of precopulatory males. J. Fish. Res. Board Can. 29:423-427.

CAREY, A. G., AND H. HEYAMOTO.
1972. Techniques and equipment for sampling benthic organisms. *In* A. T. Pruter and D. L. Alverson (editors), Columbia River estuary and adjacent ocean waters: Bioenvironmental studies, p. 378-412. Univ. Wash. Press, Seattle.

CHILDRESS, J. J., AND M. H. PRICE.
1978. Growth rate of the bathypelagic crustacean *Gnathophausia ingens* (Mysidacea: Lophogastridae). I. Dimensional growth and population structure. Mar. Biol. (Berl.) 50:47-62.

DONALDSON, W. E., R. T. COONEY, AND J. R. HILSINGER.
1981. Growth, age and size at maturity of tanner crab, *Chionoecetes bairdi* M. J. Rathbun, in the northern Gulf of Alaska (Decapoda, Brachyura). Crustaceana 40:286-302.

GOULD, S. J.
1966. Allometry and size in ontogeny and phylogeny. Biol. Rev. 41:587-640.

HARTNOLL, R. G.
1969. Mating in the Brachyura. Crustaceana 16:161-181.

HILSINGER, J. R., W. E. DONALDSON, AND R. T. COONEY.
1975. The Alaskan snow crab, *Chionoecetes bairdi*, size and growth. Univ. Alaska Sea Grant Rep. No. 75-12, Inst. Mar. Sci., 75-6 p.

LOUGH, R. G.
1974. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oregon State Univ., Corvallis, 299 p.

LUX, F. E., A. R. GANZ, AND W. F. RATHJEN.
1982. Marking studies on the red crab (*Geryon quinquedens*) Smith off southern New England. J. Shellfish. Res. 2:71-80.

MILLER, R. J., AND J. WATSON.
1976. Growth per molt and limb regeneration in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 33: 1644-1649.

PEREYRA, W. T.
1966. The bathymetric and seasonal distribution, and reproduction of adult tanner crabs, *Chionoecetes tanneri* Rathbun (Brachyura: Majidae), off the northern Oregon coast. Deep-Sea Res. 13:1185-1205.
1968. Distribution of juvenile tanner crabs (*Chionoecetes tanneri*) Rathbun, life history model, and fisheries management. Proc. Natl. Shellfish. Assoc. 58:66-70.
1972. Bathymetric and seasonal abundance and general ecology of the tanner crab, *Chionoecetes tanneri* Rathbun (Brachyura: Majidae) off the northern Oregon coast. *In* A. T. Pruter and D. L. Alverson (editors), Columbia River estuary and adjacent ocean waters: Bioenvironmental studies, p. 538-582. Univ. Wash. Press, Seattle.

RATHBUN, M. J.
1925. The spider crabs of America. Bull. U.S. Natl. Mus. 129, 613 p.

SINDERMANN, C. J.
1970. Principal diseases of marine fish and shellfish. Acad. Press, N.Y., 369 p.

SOMERTON, D. A.
1981. Regional variation in the size of maturity of two species of tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can. J. Fish. Aquat. Sci. 38:163-174.

TESSIER, G.
1960. Relative growth. *In* T. Waterman (editor), The physiology of Crustacea, Vol. 1, p. 537-560. Acad. Press, N.Y.

U.S. NATIONAL MARINE FISHERIES SERVICE.
1985. Fisheries of the United States, 1984. U.S. Natl. Mar. Fish. Serv., Curr. Fish. Stat. 8360, 121 p.

WATSON, J.
1970. Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27:1607-1616.

NOTES

COMPARISON OF CATCHES IN 4.3 M AND 12.2 M SHRIMP TRAWLS IN THE GULF OF MEXICO

Shrimp trawls used to assess shrimp and fish populations in the southern United States have varied in length, width, and basic design, making comparisons of results among studies difficult. Fishery management plans by State and Federal agencies emphasize the need for data that can be reliably compared. Techniques and equipment necessary to measure trawl performance so that data collected with different trawls can be compared is costly and time consuming (Watson 1976; Loesch et al. 1976; Wathne 1977; Kjelson and Johnson 1978). Recent emphasis has been placed on standardizing gear and sampling methods (Watson and Bane 1985) and determining the effects on catch and mean length of organisms for different tow durations, mesh sizes, trawl widths, and towing vessels (Clark 1963; Chittenden and Van Engle 1972; Green and Benefield 1982; Matthews 1982; Cody and Fuls 1985). However, sample sizes generally have been small and only selected species have been analyzed.

The present study evaluates small trawls as population sampling devices for penaeid shrimp and other organisms in the Gulf of Mexico. The objective of this study was to compare the catch rates and mean lengths of organisms caught with 4.3 m and 12.2 m trawls pulled during day and night.

Materials and Methods

The study area was the Gulf of Mexico off Texas between the Colorado River and Port Mansfield in depths from 7 m to 24 m (Fig. 1). Sample sites were established in 1° latitude by 1° longitude grids within the study area. Twenty randomly selected sites were sampled monthly from November 1982-February 1983. Samples were equally and randomly distributed between day and night.

At each site two trawls were towed simultaneously for 15 min at approximately 3 kn from the Texas Parks and Wildlife Department (TPWD) RV *Western Gulf*, a double-rigged 21.9 m steel-hull shrimp trawler. The 4.3 m trawl (small net) was spread by wooden trawl doors 0.4 m high and 0.8 m long and the 12.2 m wide trawl (large net) was spread by wooden trawl doors 0.9 m high and 2.1 m long. Both nets had 5.1 cm stretched mesh webbing in the body, 4.4 cm mesh in the bag, and were equipped with tickler chains.

Trawl catches weighing ≤10 kg were processed by identifying and counting all organisms in the catch. For larger catches a 10 kg subsample was randomly selected from the total catch, and the total number for each species was estimated by dividing subsample counts by the proportion of subsample weight to total weight. Total lengths were measured on no more than 50 individuals of each *Penaeus* shrimp species and no more than 20 individuals of all other species. The arithmetic mean for length data was calculated for each species in each sample.

The relationship between number caught (or mean length) in the two trawls was tested for linear, multiplicative and exponential models, and log and square root transformations (Sokal and Rohlf 1981). No significant improvement was found over a linear regression with no transformation. Mean length regressions were developed for species with 10 or more pairs of mean length data (≥2 measurements) in each size of trawl (Fig. 2). Catch regressions were developed for those species that were present in at least 20 samples in the large net and were represented by at least 5 samples with >20 individuals in the small net. This insured a sufficiently wide distribution to yield meaningful results (Fig. 3).

Differences ($P \leq 0.01$) between day and night regressions for each species were evaluated using analysis of covariance (Snedecor and Cochran 1980).

Results

Small trawls can be used to obtain trend data on mean lengths of species caught in offshore waters. Relationships exist between the catch in the 4.3 m trawl vs. the catch in the 12.2 m trawl. No significant differences were found in the day-night regressions of mean length for any species tested. There was no difference in the day-night catch vs. catch relationship for total organisms or *Penaeus setiferus* but one did exist for *Trachypenaeus* sp. and *Squilla empusa*.

Mean lengths in the two trawls were directly correlated for all species that met criteria for regression analysis (Table 1). The regressions of the mean length of fish caught in one net vs. the other for day and night were not significantly different for any

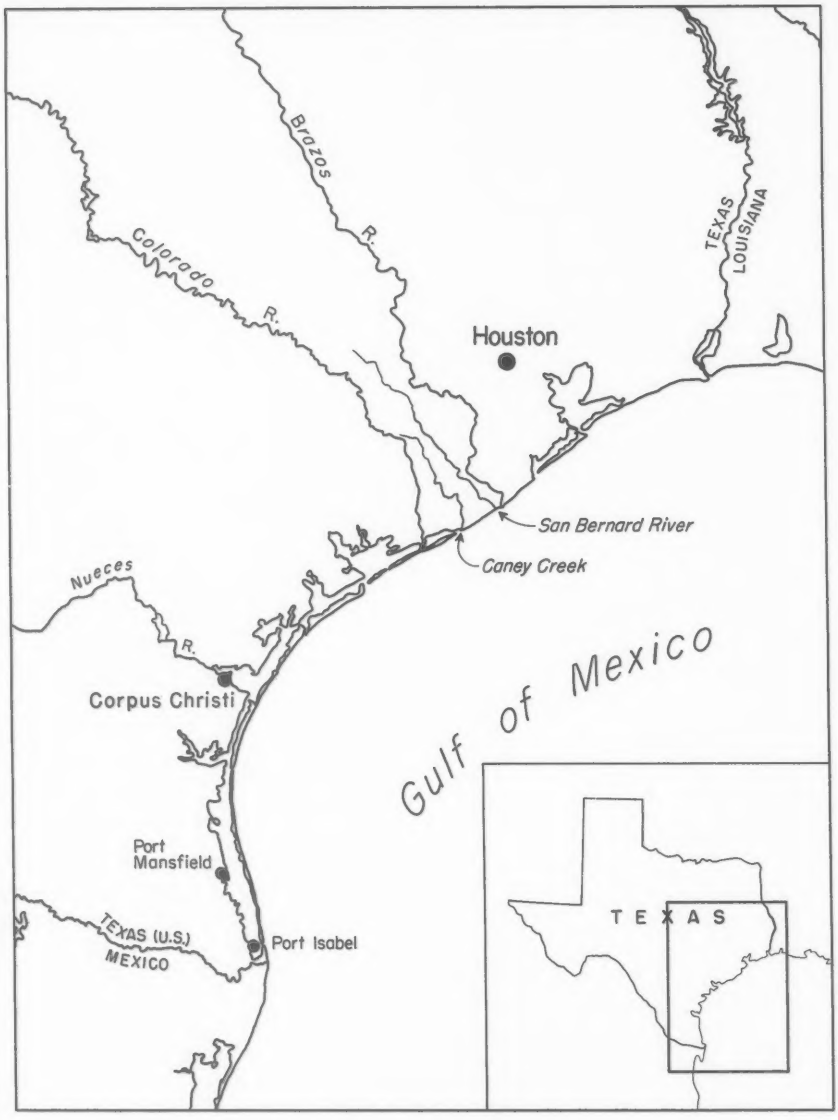

FIGURE 1.—Gulf of Mexico sampling area off the Texas coast for 4.3 m and 12.2 m trawls towed simultaneously during November 1982-February 1983.

of the species tested (Table 2). The combined regressions had significant positive correlations (0.51-0.89) explaining 26-79% of the variation.

Catch per tow in the two trawls was positively correlated. Correlation coefficients (0.48-0.93) were significant for all species meeting the criteria for analysis (Table 3). The percent of variation explained (r^2) varied from 23 to 86%.

There were no significant differences in the day-night catch vs. catch relationships for total organ-

TABLE 1.—Linear regression results of 4.3 m trawl mean length (X_i) versus the 12.2 m trawl length (Y_i) for selected species.

Species	Time	Range of X_i	Number	Y-intercept	Slope (b)	Correlation coefficient	$S^2\ Y \cdot X$	95% confidence interval of b
Penaeus setiferus	Day	93-135	29	12.31	0.91	0.85**	61.33	0.68-1.13
	Night	94-164	32	16.29	0.87	0.93**	22.98	0.74-1.00
	Combined	93-164	61	14.48	0.89	0.88**	39.86	0.76-1.01
Stellifer lanceolatus	Day	44-125	11	26.35	0.70	0.91**	88.77	0.45-0.95
	Night	44-115	24	28.32	0.67	0.88**	65.60	0.51-0.83
	Combined	44-125	35	27.42	0.68	0.89**	68.19	0.56-0.80
Trachypenaeus sp.	Day	50-78	22	38.03	0.47	0.61**	17.55	0.18-0.76
	Night	50-84	36	43.03	0.40	0.61**	19.28	0.22-0.58
	Combined	50-84	58	41.77	0.42	0.62**	18.03	0.28-0.56
Portunus gibbesii	Day	30-48	14	26.44	0.39	0.53*	11.78	−0.01-0.78
	Night	30-55	30	23.81	0.41	0.62**	9.70	0.21-0.61
	Combined	30-55	44	25.43	0.38	0.56**	10.53	0.21-0.56
Squilla empusa	Day	77-104	10	49.37	0.46	0.62ns	48.08	0.04-0.89
	Night	48-132	31	69.43	0.32	0.51**	86.95	0.11-0.52
	Combined	48-132	41	65.78	0.34	0.51**	83.87	0.15-0.53
Cynoscion nothus	Day	62-110	25	52.02	0.42	0.63**	43.87	0.20-0.64
	Night	70-122	21	45.59	0.44	0.71**	30.64	0.23-0.65
	Combined	62-122	46	46.18	0.46	0.67**	42.16	0.31-0.62

*$P < 0.05$.
**$P < 0.01$.

TABLE 2.—Summary of ANCOVA for mean length of selected species.

Species	df	Calculated F_s for H_0:$\alpha_1 = \alpha_2$	df	Calculated F_s for H_0:$\beta_1 = \beta_2$	df	Calculated F_s for H_0:$\alpha_1 = \alpha_2$
Penaeus setiferus	(27,30)	2.67 ns	(1,57)	0.04 ns	(1,58)	0.07 ns
Stellifer lanceolatus	(9,22)	1.35 ns	(1,31)	0.03 ns	(1,32)	0.04 ns
Trachypenaeus sp.	(34,20)	1.10 ns	(1,54)	0.09 ns	(1,55)	0.00 ns
Portunus gibbesii	(12,28)	1.22 ns	(1,40)	0.00 ns	(1,41)	2.89 ns
Squilla empusa	(29,8)	1.81 ns	(1,37)	0.15 ns	(1,38)	4.46 ns
Cynoscion nothus	(23,19)	1.43 ns	(1,42)	0.01 ns	(1,43)	7.12 ns

TABLE 3.—Linear regression results of 4.3 m trawl catch/tow (X_i) versus the 12.2 m trawl catch/tow (Y_i) for total organisms and selected species.

Species	Time	Range of X_i	Number	Y-intercept	Slope (b)	Correlation coefficient	$S^2\ Y \cdot X$	95% confidence interval of b
Total organisms	Day	16-212	40	352.71	5.83	0.58**	143,234.17	3.18-8.47
	Night	43-210	40	593.65	6.04	0.48**	310,412.80	2.45-9.64
	Combined	16-212	80	420.42	6.53	0.55**	237,569.91	4.31-8.75
Penaeus setiferus	Day	0-55	40	12.21	5.37	0.90**	1,129.54	4.51-6.23
	Night	0-51	39	−0.87	6.96	0.87**	2,291.77	5.65-8.26
	Combined	0-55	79	7.40	6.14	0.88**	1,757.99	5.38-6.90
Squilla empusa	Day	0-28	40	6.03	4.50	0.93**	139.44	3.92-5.07
	Night	0-37	39	−5.58	6.81	0.85**	1,438.75	5.38-8.25
Trachypenaeus sp.	Day	0-45	40	20.63	13.38	0.80**	13,040.70	10.15-16.60
	Night	0-43	40	60.23	19.51	0.73**	40,354.41	13.46-25.67
Portunus gibbesii	Night	0-114	40	24.65	5.92	0.78**	9,961.84	4.40-7.45
Lolliguncula brevis	Day	0-42	40	9.92	1.66	0.72**	292.57	1.14-2.19

**$P < 0.01$.

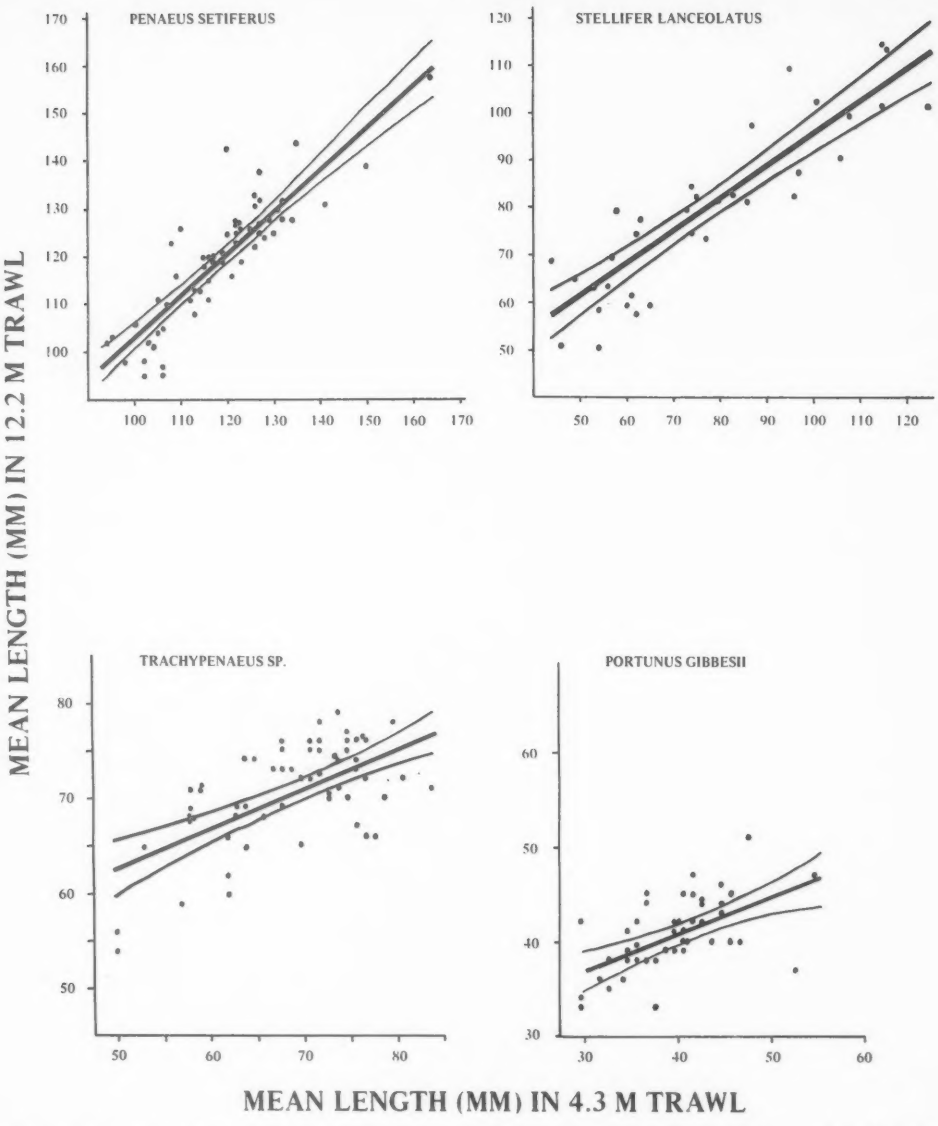

FIGURE 2.—Regression of mean length in 12.2 m trawl (Y_i) on mean length in 4.3 m trawl (X_i) for comparative tows during November 1982-February 1983. Observations, regression line, and 95% confidence intervals are shown.

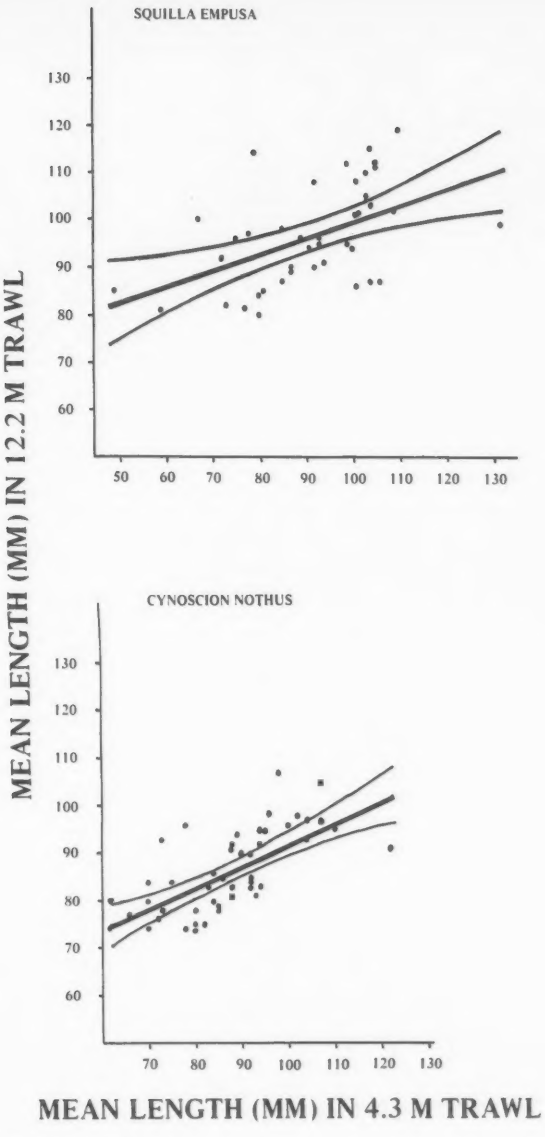

FIGURE 2.—*Continued.*

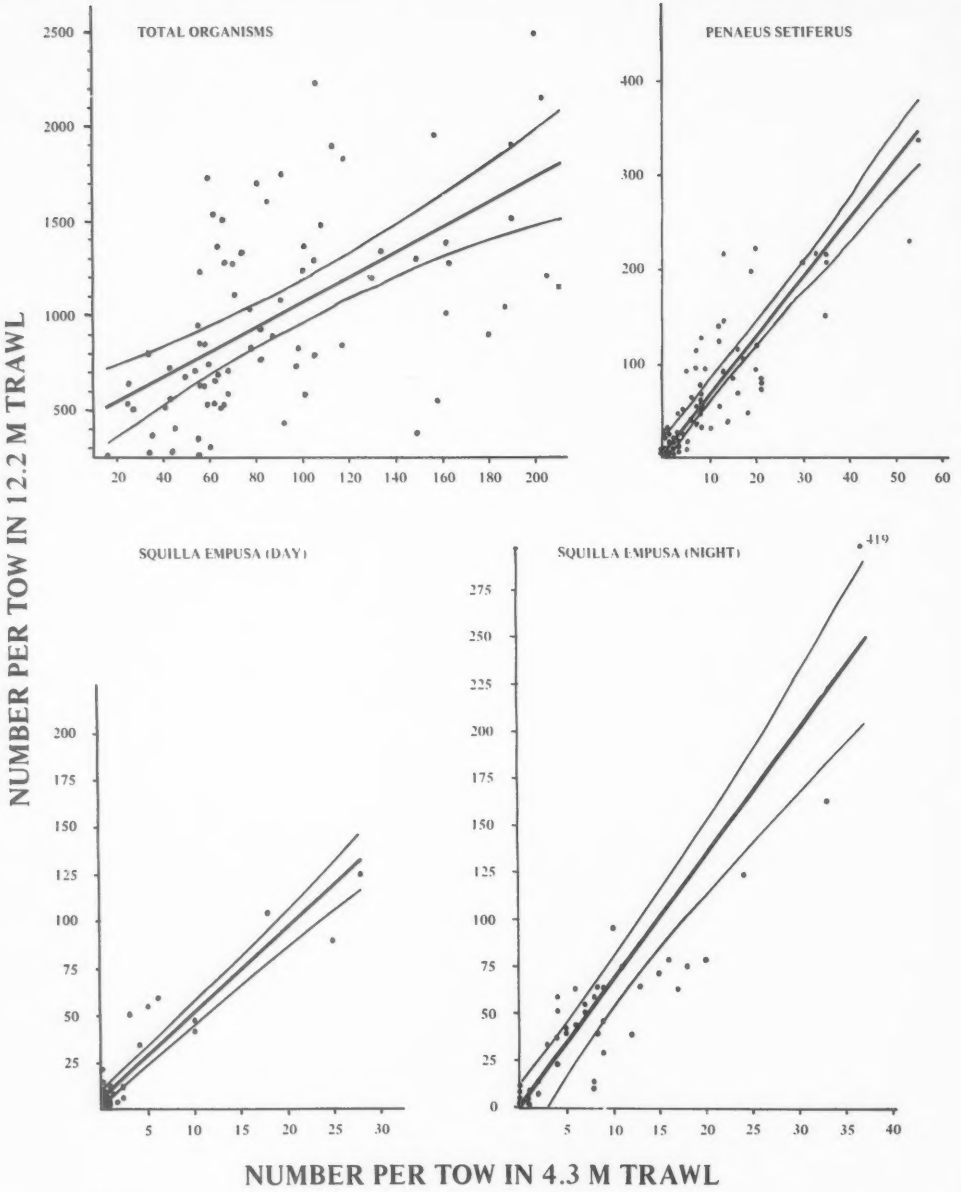

FIGURE 3.—Regression of catch per tow in 12.2 m trawl (Y_i) on catch per tow in 4.3 m trawl (X_i) for comparative tows during November

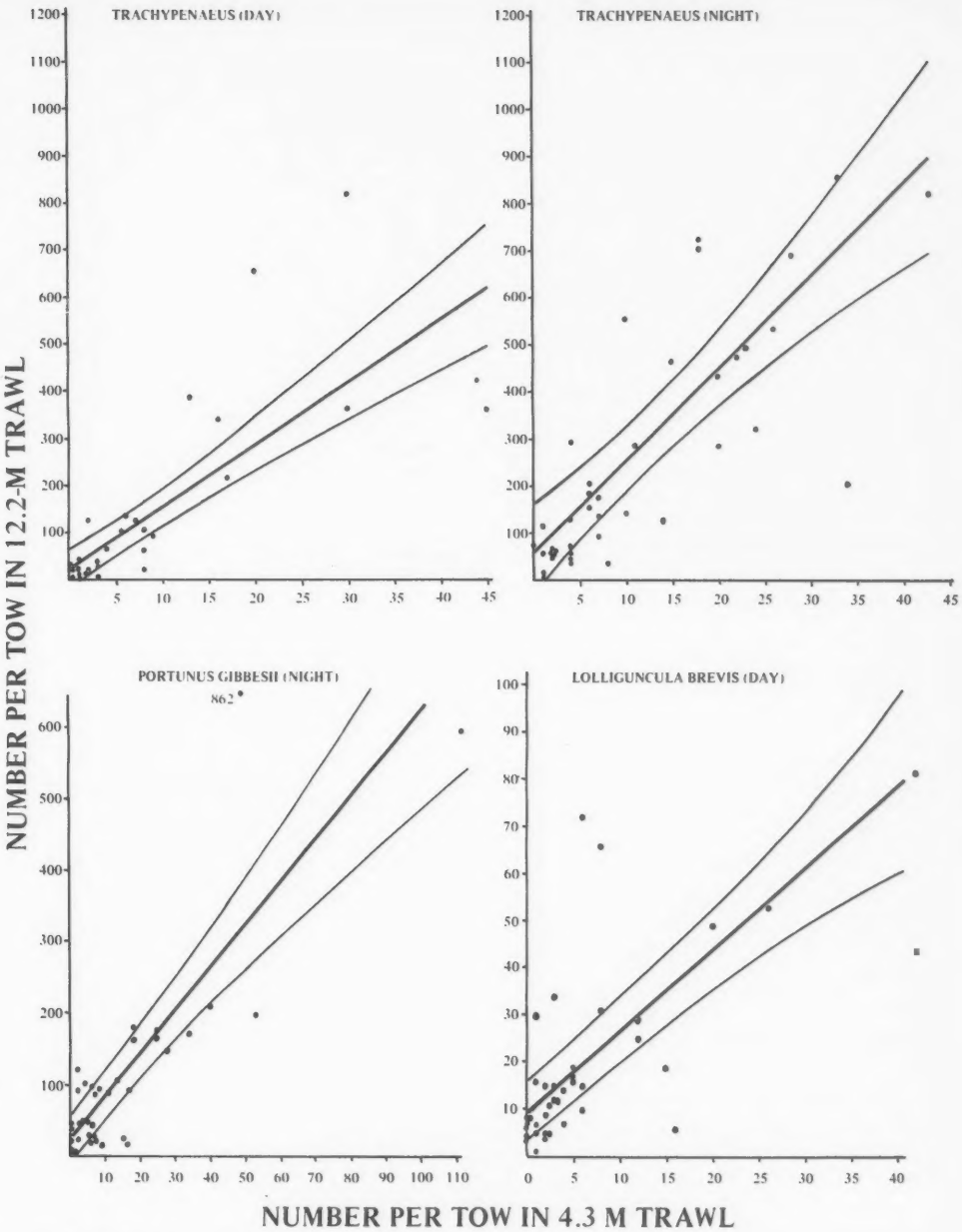

FIGURE 3.—*Continued.*—1982-February 1983. Observations, regression line, and 95% confidence intervals are shown.

isms or *P. setiferus*. Significantly different residual variances were found for *S. empusa* and *Trachypenaeus* sp. (Table 4).

The 12.2 m trawl caught more individuals and more species than the 4.3 m trawl (Table 5). The large trawl caught 30,000 organisms during the day and 46,000 during the night. The small trawl caught 3,000 during the day and 3,800 during the night. The large trawl caught 99 species during the day and 107 during the night, while the small trawl caught 63 species during the day and 82 during the night. The trend of more species caught in the large trawl was apparent for vertebrates both day and night and invertebrates during the day. The same number of invertebrate species were caught at night in both trawls. Species caught exclusively in one trawl were usually represented by fewer than 30 individuals during the entire study.

Only 26 of 125 species were represented by a mean catch ⩾5/tow in either trawl (Table 6). These 26 species comprised 95% of the total catch.

small trawl it was 0.03. The fishery manager must decide if an increase in species diversity helps manage a particular fishery and ultimately whether it is cost effective to go after these "rare" individuals.

Catch in the large trawl may be higher than in the small trawl because of higher efficiency. Kjelson and Johnson (1978) reported higher catch efficiencies for a 6.1 m trawl than for a 3.0 m or 4.6 m trawl. Loesch et al. (1976) reported 5% efficiency for *Leiostomus xanthurus* in a 4.0 m trawl while Kjelson and Johnson (1978) reported 32% for the same species in a 6.1 m trawl.

The relationship between trawl width and catch may be asymptotic. This study showed the 12.2 m trawl caught more organisms than the 4.3 m trawl. Cody and Fuls (1985) found the same trend but reported that the catch in the 12.2 m trawl was not significantly less than the catch in the 13.7 m trawl. Matthews (1982) found no difference in mean total weight caught in 12.2 m and 13.7 m trawls. He did

TABLE 4.—Summary of ANCOVA for catch per tow of total organisms and selected species.

Species	df	Calculated F_s for H_0:$\alpha_1 = \alpha_2$	df	Calculated F_s for H_0:$\beta_1 = \beta_2$	df	Calculated F_s for H_0:$\alpha_1 = \alpha_2$
Total organisms	(38,38)	2.17 ns	(1,76)	0.01 ns	(1,77)	5.76 ns
Penaeus setiferus	(37,38)	2.03 ns	(1,75)	4.32 ns	(1,76)	0.16 ns
Squilla empusa	(37,38)	10.32 **				
Trachypenaeus sp.	(38,38)	3.09 **				

**$P < 0.01$.

Discussion

Catches in the large trawl were consistently higher than in the small trawl. Chittenden and Van Engel (1972) stated there must be some relationship between catch and tow duration because of the amount of bottom sampled, but they found that increased tow duration (which increases area covered) did not significantly increase the catch of blue crabs in a 9.1 m trawl. However, they tested only a small range of tow durations (5-15 min) and concluded that variation in the trawl catches was a significant factor. Tow duration in this study was constant, so higher catches were most likely a result of more area being sampled by the larger net.

It also seems reasonable that a large trawl would have a greater chance of encountering organisms especially if they have patchy distributions such as found with shrimp (Matthews 1982). The large net caught more species than the small net in this study. The highest mean catch per tow was 0.37 for species found exclusively in the large trawl; for the not, however, compare the total number or size of organisms. Because of the inherent variation found in sampling with trawls, the inability to detect differences in the 12.2 m and 13.7 m trawls would be expected.

Implications of this may apply to the commercial trawl fishery. Through the years shrimp fishermen have been reducing the size of trawls and increasing the number of trawls used in order to increase catch efficiency (Christmas and Etzold 1977). These changes may reflect the asymptotic relationship of trawl width and at the same time help reduce unwanted bycatch.

Cody and Fuls (1985) reported a regression coefficient of 2.52 for the catch vs. catch relationship for *P. setiferus* in daytime samples in contrast to 5.37 for this study. Only 13 data points over a much wider range of X_i (0-136/tow vs. 0-55/tow) were used by Cody and Fuls. When the ranges of X_i were made comparable the slopes of the two regressions were not significantly different.

The use of small trawls and determination of rela-

TABLE 5.—Total number of organisms collected with 4.3 m and 12.2 m trawls towed simultaneously off the central Texas coast from November 1982-February 1983. Blanks = no data.

Species	Day		Night	
	4.3 m	12.2 m	4.3 m	12.2 m
Vertebrates				
Cynoscion nothus	257	8,781	190	8,981
Stellifer lanceolatus	80	1,110	333	4,559
Cynoscion arenarius	48	1,383	46	2,498
Peprilus burti	106	1,903	20	344
Leiostomus xanthurus	118	1,510	9	68
Arius felis	77	775	17	283
Symphurus plagiusa	40	297	60	470
Lagodon rhomboides	43	357	36	350
Syacium gunteri	29	400	29	235
Anchoa mitchilli	16	372	12	222
Larimus fasciatus	30	188	31	356
Menticirrhus americanus	9	164	23	315
Micropogonias undulatus	23	218	17	237
Trichiurus lepturus	6	309	3	167
Selene setapinnis	16	269	4	88
Sphoeroides parvus	17	162	16	178
Orthopristis chrysoptera	14	87	19	133
Peprilis alepidotus	8	91	4	77
Menticirrhus littoralis	8	66	2	100
Etropus crossotus	5	37	16	116
Prionotus salmonicolor	4	10	6	137
Astroscopus y-graecum	1	37	11	93
Brevoortia patronus	1	6	2	124
Prionotus tribulus	9	43	12	63
Chloroscombrus chrysurus		28	4	87
Hemicaranx amblyrhynchus	1	63	2	26
Citharichthys spilopterus	8	21	16	43
Halieutichthys aculeatus	6	10	8	62
Urophycis floridanus	5	27	6	38
Achirus lineatus	2	26		27
Dasyatis sabina	1	19		32
Synodus foetens		28	1	13
Ophidion welshi	1	7	4	25
Porichthys plectrodon		11	2	24
Trachurus lathami		28		2
Anchoa hepsetus		24		
Saurida brasiliensis		16		3
Paralichthys lethostigma		12		6
Chaetodipterus faber		10	3	4
Opisthonema oglinum		15		2
Lutjanus campechanus		2	3	11
Bairdiella chrysoura	1	9	1	5
Chilomycterus schoepfi		9		5
Ogcocephalus parvus		3	4	6
Centropristis philadelphica	1	4		8
Monacanthus hispidus		4	3	5
Bollmannia communis		5		4
Rhinoptera bonasus		6		3
Paralichthys albigutta	1	5		3
TRIGLIDAE (Unidentified)			4	4
Lepophidium graellsi			1	7
Pomatomus saltatrix		1	1	6
Selene vomer		4		4
Gymnachirus texae		3	1	3
Polydactylus octonemus		4		1
Narcine brasiliensis				5
Eucinostomus gula		3		2
Serranus atrobranchus		2		2
Sygnathus scovelli		2	1	1
Ophidion grayi				3
Pogonias cromis		1		2
Mugil cephalus				2
Serraniculus pumilio				2
Ancylopsetta quadrocellata		2		
Membras martinica				2
Prionotus rubio		2		
Sardinella aurita		1		
Diplectrum bivittatum				1
Eucinostomus argenteus		1		
Raja texana				1
Bregmaceros atlanticus				1
Ogcocephalus radiatus		1		
GERREIDAE (Unidentified)				1
Bagre marinus				1
Lutjanus apodus			1	
Prionotus ophryas		1		
Total	992	18,995	984	20,699
Invertebrates				
Trachypenaeus sp.	297	4,798	467	11,522
Penaeus setiferus	347	2,352	594	4,180
Portunus gibbesii	113	876	561	4,332
Squilla empusa	115	758	390	2,173
Lolliguncula brevis	304	902	25	515
Callinectes similis	73	447	109	1,013
Renilla mulleri	157	379	218	369
Stomolophus melaegris	165	486	24	294
Penaeus duorarum	7	54	34	298
Sicyonia dorsalis		19	36	280
Portunus spinimanus	6	16	42	263
Brissopsis alta	181	58	35	36
ACTINIARIA (order)	31	42	62	133
Arenaeus cribrarius		15	60	139
Astropecten antillensis	110	54	30	21
Luidia clathrata	33	21	61	61
Xiphopeneus kroyeri	11	109		5
Penaeus aztecus	7	70	2	44
Aurelia aurita	16	52		6
Libinia dubia	9	19	9	28
Millita quinquiesperforata	1	21	33	1
Persephona aquilonaris	9	2	20	9
Sequilla neglecta	6	3	5	16
Libinia emarginata		7	3	17
Ovalipes guadulpensis	5	9	4	6
Hepatus epheliticus	4	2	6	11
Persephona crinita	3	2	12	4
Dactylometra quinquecirrha		4		12
Luidia alternata	1	10	2	3
Polinices duplicatus	2	1	6	6
Loligo peali	1	7	1	1
Calappa sulcata	2	5		2
Sicyonia brevirostris			1	6
Phalium granulatum			4	1
Squilla chydaea				3
Thais haemostoma	1		2	
Callinectes sapidus		1		1
Anadara ovalis			2	
Albunea paretii			1	1
Dinocardium robustum			1	1
Synalpheus fritzmuelleri			1	
Hepatus pudibundus		1		
Mnemiopsis mccradyi		1		
Architectonica nobilis			1	
Busycon perversum			1	
Calappa flammea				1
Portunus spinicarpus			1	
Sinum perspectivum			1	
REPTANTIA (suborder)		1		
Total	2,017	11,604	2,867	25,814
Grand Total	3,009	30,599	3,851	46,513

TABLE 6.—Mean catch per tow (±1 SE) of dominant species[1], November 1982-February 1983. Blank = no catch.

Species	Day		Night	
	4.3 m	12.2 m	4.3 m	12.2 m
Vertebrates				
Cynoscion nothus	6 ± 1.2	219 ± 43.0	5 ± 0.9	225 ± 33.6
Stellifer lanceolatus	2 ± 0.7	28 ± 12.0	8 ± 2.6	114 ± 29.8
Cynoscion arenarius	1 ± 0.3	34 ± 7.7	1 ± 0.2	62 ± 14.5
Peprilus burti	3 ± 1.0	47 ± 16.1	0 ± 0.3	9 ± 2.9
Leiostomus xanthurus	3 ± 1.9	38 ± 27.9	0 ± 0.1	2 ± 0.7
Arius felis	2 ± 1.8	20 ± 18.0	0 ± 0.3	7 ± 3.4
Symphurus plagiusa	1 ± 0.3	7 ± 2.1	2 ± 0.3	12 ± 2.0
Lagodon rhomboides	1 ± 0.6	9 ± 4.7	1 ± 0.3	9 ± 3.2
Syacium gunteri	1 ± 0.2	10 ± 2.6	1 ± 0.2	6 ± 1.6
Anchoa mitchilli	0 ± 0.2	9 ± 4.0	0 ± 0.2	6 ± 2.4
Larimus fasciatus	1 ± 0.4	5 ± 2.2	1 ± 0.3	9 ± 3.7
Menticirrhus americanus	0 ± 0.1	4 ± 1.3	1 ± 0.2	8 ± 1.7
Micropogonias undulatus	1 ± 0.2	5 ± 1.4	0 ± 0.2	6 ± 1.4
Trichiurus lepturus	0 ± 0.1	8 ± 2.1	0 ± 0.0	4 ± 0.9
Selene setapinnis	0 ± 0.3	7 ± 5.8	0 ± 0.0	2 ± 1.5
Invertebrates				
Trachypenaeus sp.	7 ± 1.8	120 ± 30.1	11 ± 1.7	228 ± 45.6
Penaeus setiferus	9 ± 2.0	59 ± 11.9	15 ± 3.1	104 ± 24.2
Portunus gibbesii	3 ± 1.1	2 ± 4.4	14 ± 3.3	108 ± 25.2
Squilla empusa	3 ± 1.0	19 ± 5.0	10 ± 1.7	54 ± 10.9
Lolliguncula brevis	8 ± 1.7	23 ± 3.8	1 ± 0.2	13 ± 1.9
Callinectes similis	2 ± 0.8	11 ± 4.6	3 ± 0.6	25 ± 6.0
Renilla mulleri	4 ± 1.5	9 ± 3.0	5 ± 2.2	9 ± 3.3
Stomolophus melaegris	4 ± 3.4	12 ± 6.0	1 ± 0.3	7 ± 3.0
Penaeus duorarum	0 ± 0.1	1 ± 0.6	1 ± 0.4	7 ± 5.0
Sicyonia dorsalis		0 ± 0.3	1 ± 0.3	7 ± 2.0
Portunus spinimanus	0 ± 0.1	0 ± 0.2	1 ± 0.6	7 ± 2.9

[1]Mean catch ≥5/tow in either net.

tionships between day and night catches in a fishery independent assessment program can increase sampling frequency and decrease the cost of sampling by reducing processing time, manpower requirements, and variability caused by subsampling large catches. Samples from the small trawl could be processed in approximately 25% of the time required for sample processing from the large trawl. The small trawl required no subsampling. Management agencies should consider these findings when planning long-term programs.

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Literature Cited

CHITTENDEN, M. E., JR., AND W. A. VAN ENGEL.
1972. Effect of a tickler chain and tow duration on trawl catches of the blue crab, *Callinectes sapidus*. Trans. Am. Fish. Soc. 101:732-734.

CHRISTMAS, J. Y., AND D. J. ETZOLD.
1977. The shrimp fishery of the Gulf of Mexico United States: a regional management plan. Gulf Coast Res. Lab., Ocean Springs, MS, Tech. Rep. Ser. No. 2, 128 p.

CLARK, J. R.
1963. Size selection of fish by otter trawls. Results of recent experiments in the Northwest Atlantic. D. Effect of duration of tow on codend escapement. Int. Comm. Northwest Atl. Fish. Spec. Pub. 5, p. 55-58.

CODY, T. J., AND B. E. FULS.
1985. Comparison of the catch rates of three trawls in offshore Texas waters. *In* J. W. Watson and N. Bane (editors), Proceedings of the SEAMAP shrimp and bottomfish sampling gear workshop, p. 19-29. Gulf States Mar. Fish. Comm. No. 12.

GREEN, A. W., AND R. L. BENEFIELD.
1982. Mesh size selectivity study of penaeid shrimp trawled from Galveston Bay, Texas May 1981. Tex. Parks Wildlf. Dep., Coast. Fish. Branch, Manage. Data Ser. No. 40, 9 p.

KJELSON, M. A., AND G. N. JOHNSON.
1978. Catch efficiencies of a 6.1-meter otter trawl for estuarine fish populations. Trans. Am. Fish. Soc. 107:246-254.

LOESCH, H., J. BISHOP, A. CROWE, R. KUCKYR, AND P. WAGNER.
1976. Technique for estimating trawl efficiency in catching brown shrimp (*Penaeus aztecus*), Atlantic croaker (*Micropogon undulatus*) and spot (*Leiostomus xanthurus*). Gulf

Res. Rep. 5(2):29-33.
MATTHEWS, G. A.
1982. Relative abundance and size distributions of commercially important shrimp during the 1981 Texas closure. Mar. Fish. Rev. 44(9-10):5-15.
SNEDECOR, G. W., AND W. G. COCHRAN.
1980. Statistical methods. 7th ed. Iowa State Univ. Press., Ames, 507 p.
SOKAL, R. R., AND F. J. ROHLF.
1981. Biometry: The principles and practices of statistics in biological research. 2d ed. W. H. Freeman and Co., San Francisco, 859 p.
WATHNE, F.
1977. Performance of trawls used in resource assessment. Mar. Fish. Rev. 39(6):16-23.
WATSON, J. W., JR.
1976. Electric shrimp trawl catch efficiency for *Penaeus duorarum* and *Penaeus aztecus*. Trans. Am. Fish. Soc. 105: 135-148.
WATSON, J. W., JR., AND N. BANE (editors).
1985. Proceedings of the SEAMAP shrimp and bottomfish sampling gear workshop. Gulf States Mar. Fish. Comm. No. 12, 80 p.

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EARLY LIFE HISTORY OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, AND GULF MENHADEN, *B. PATRONUS*

Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*, are allopatric, morphologically similar clupeids with contrasting distributional patterns and reproductive traits. The Atlantic menhaden has a meridional distribution and encounters variable environmental conditions during its lifetime. It occurs along the eastern coast of North America from Nova Scotia to Florida, and its distribution is stratified by age and size, with the older and larger fish ranging farther north (Nicholson 1978). Atlantic menhaden are a relatively long-lived clupeid. Their maximum reported age is approximately 10 yr, and they may spawn for approximately 7 yr (Higham and Nicholson 1964; Nicholson 1975). The spatial and temporal spawning habits of Atlantic menhaden are more complex than those of its congener. In Long Island Sound and New England waters, limited spawning occurs in inshore waters during the summer and early fall. From Long Island to Chesapeake Bay, spawning occurs in offshore coastal waters from October to December and from March to May. From North Carolina to Florida, spawning occurs in offshore coastal waters from October through March and this spawning population consists of fish that have migrated from the north and contains all age groups (Nicholson 1978). The gulf menhaden, which is distributed zonally, is restricted to the Gulf of Mexico and ranges from Cape Sable, FL, to Vera Cruz, Mexico (Reintjes 1969). Their maximum reported age is approximately 4 yr, and they may spawn for approximately 2 yr (Lewis and Roithmayr 1981). They spawn from October through March in nearshore and offshore waters within the 110 m depth contour (Christmas and Waller 1975). Both species use estuaries as nursery areas for more than half their first year of life.

The major objectives of this study were to examine and compare early life history characteristics of these two menhadens and to investigate the effects of temperature on developmental processes. Characteristics examined were egg size, size at hatching, yolk utilization rates, yolk volume at first feeding, size and age at first feeding, and growth.

Methods

Atlantic menhaden were collected with a commercial purse seine from the Newport River, NC, during the summer. Fish were held in the laboratory at ambient temperatures for approximately 4 mo before spawning. Gulf menhaden were collected in late September by cast net near Gulf Breeze, FL, and transported to the laboratory by methods developed by Hettler (1983). They were held in the laboratory at ambient temperatures for about 1 mo before spawning. For each spawning, about 10 menhaden were induced to spawn by methods described by Hettler (1981, 1983). Eggs were spawned in approximately 20°C water during the night and collected the following morning. All experiments except those dealing specifically with growth were conducted in 10 L rearing tanks; growth experiments were conducted in 60 L rearing tanks. Tanks were set in a temperature controlled water bath with two 40-W fluorescent lamps positioned 40 cm above each tank, and the tanks were illuminated for 12 h daily. Temperatures were controlled to approximately ±0.5°C. Salinities ranged from 28‰ to 32‰. Rotifers, *Brachionus plicatilis*, were used as food for about the first 10 d, and *Artemia* nauplii and rotifers were used thereafter. Feeding levels were not controlled, but, based on experience, we pro-

vided food in densities we felt would not limit growth.

Growth in standard length (SL) from the time larvae begin feeding to age 21 d at 20°C was modeled by an exponential equation. All measurements were made on eggs and larvae that were preserved in 5% sodium acetate buffered Formalin[1]. Volumes (V) of the elliptically shaped yolk mass were calculated using the formula for a prolate spheroid

$$V = (\pi/6)\, lh^2,$$

where l is the length and h is the height of the yolk mass (Blaxter and Hempel 1963).

We were unable to treat the two species the same in most experiments. The gulf menhaden was subjected to a greater number of treatments than the Atlantic menhaden. Experiments dealing with starvation and yolk utilization rates were conducted only on the gulf menhaden. In addition, the lack of replications for some experiments limited the application of statistical tests (e.g., ANOVA) and, as a result the differences or similarities between the two menhadens, should be considered tentative.

Results and Discussion

Based on a sample of eggs from the single spawn of a group of approximately five females from each species, Atlantic menhaden had significantly ($P < 0.001$) larger eggs (1.6 mm diameter, $N = 20$) than gulf menhaden (1.3 mm diameter, $N = 20$). Egg sizes for both these species that have been reported (Houde and Fore 1973; Jones et al. 1978; Hettler 1984) support our observations that Atlantic menhaden eggs are larger than gulf menhaden eggs. Atlantic menhaden larvae measured at hatching also were larger than gulf menhaden (Fig. 1) and supports Blaxter and Hunter's (1982) view that egg size greatly influences the size of larvae at hatching.

Temperature did not affect the size at hatching of gulf menhaden (Fig. 1), but the rate of yolk utilization was affected by temperature and was roughly 2.5 times faster at the highest temperature (24°C) than at the lowest temperature (14°C) (Table 1). The instantaneous rate of yolk utilization increased linearly with increasing temperature (Fig. 2). The volume of yolk at the onset of exogenous feeding (first feeding) was approximately similar at all temperatures (Table 1) and was not affected by temperature (ANOVA, $P = 0.13$).

The size of gulf menhaden at first feeding was independent of temperature (Fig. 3) (ANOVA $P = 0.15$) and, although data are limited, the size of Atlantic menhaden also was independent of temperature. The age at first feeding, however, was dependent on temperature (Fig. 3). An ANCOVA (log transformed ages on temperature) revealed that the regression slopes were similar ($P = 0.37$), in-

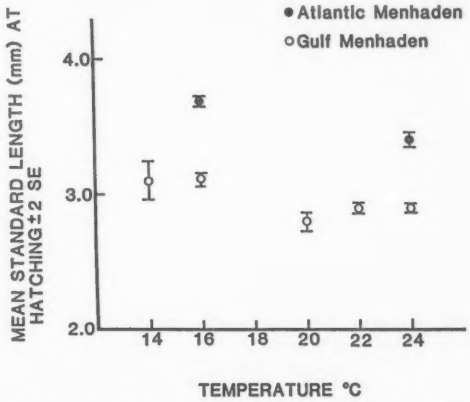

FIGURE 1.—The size at hatching of Atlantic gulf menhadens at different temperatures. Each point represents the mean of 10 fish.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—The effects of temperature on yolk utilization of gulf menhaden. For regression equations, $Y = \log_e$ preserved yolk volume (mm^3) and X = age (d). The equations were derived from the means of approximately 10 fish per sample. S is the number of samples; N is the number of larvae.

Temperature (°C)	S No.	Regression equation	r^2	Mean volume of yolk at hatching (mm^3)	N	Mean volume of yolk at first feeding (mm^3)	N
14	15	$Y = -1.189 - 0.96446(x)$	0.93	0.130482	10	0.000340	20
16				0.133397	10	0.000335	10
18	5	$Y = -0.803 - 1.67066(x)$	0.98			0.000211	10
20	10	$Y = -1.375 - 1.61365(x)$	0.91	0.169317	10	0.000549	20
22	7	$Y = -1.447 - 2.04386(x)$	0.96	0.110202	10	0.000506	20
24	8	$Y = -1.509 - 2.22355(x)$	0.95	0.123148	10	0.000289	19

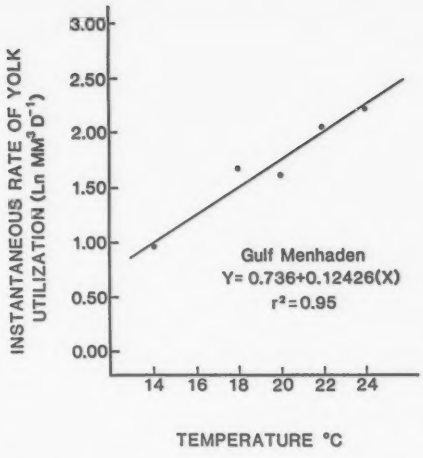

FIGURE 2.—The effects of temperature on the instantaneous rate of yolk utilization for gulf menhaden.

dicating a similar response to temperature by both species. But the *Y*-intercepts differed significantly ($P = 0.02$) indicating that, over the range of temperatures tested, the Atlantic menhaden fed at a significantly earlier age than gulf menhaden. For both species the age at first feeding declined exponentially with increasing temperatures. Atlantic menhaden were larger than the gulf menhaden at first feeding (Fig. 3). At 20°C, Atlantic and gulf menhaden growth rates were similar (ANCOVA, $P = 0.36$), but Atlantic menhaden maintained a size advantage during the early larval period (Table 2). This difference was attributed to differential size and age at first feeding.

The ability of early larvae to withstand the deprivation of food was influenced by temperature (Table 3). Although at 20°C mortalities may be attributed to causes other than starvation (compare control and starved), at progressively higher temperatures larvae are less able to withstand the deprivation of food. For example, at 24°C, gulf menhaden must find food within three days after the onset of first

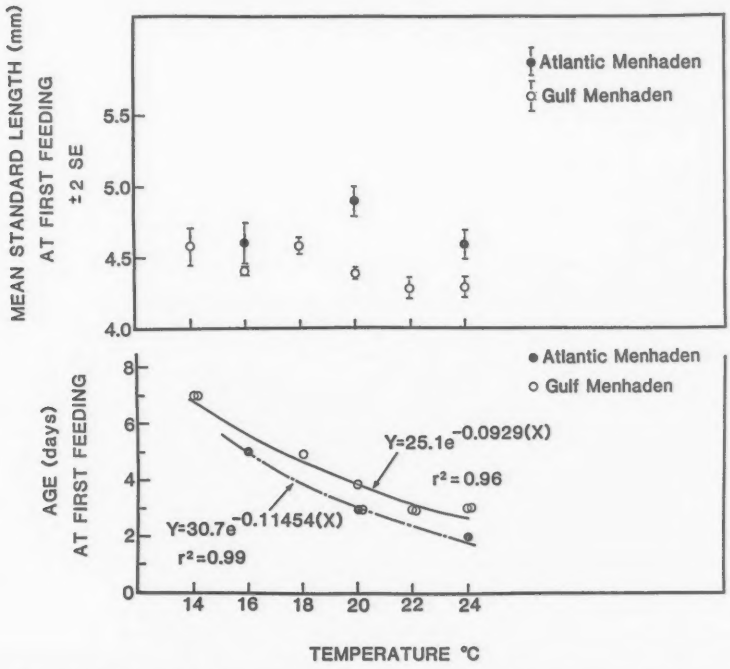

FIGURE 3.—The size and age when gulf and Atlantic menhadens begin feeding on exogenous food sources at different temperatures. Each point represents a sample of about 10 fish. Replicate experiments were only conducted for gulf menhaden and only at 14°, 20°, 22°, and 24°C.

TABLE 2.—Growth of larval gulf and Atlantic menhadens from time of first feeding to age 21 d at 20°C.

Species	N[1]	Growth parameters[2] a	b	r^2	Estimated SL (mm) First feeding	Age 21 d
Gulf menhaden	11	3.36	0.04640	0.97	4.0	8.9
Atlantic menhaden	16	4.38	0.04267	0.95	5.0	10.7

[1]Number of samples; about 10 fish per sample.
[2]SL (mm) = $a \times \exp b$ (age in d).

TABLE 3.—The survival (%) of first-feeding gulf menhaden larvae deprived of food (starved) in relation to temperature. The fed treatment represents the control group.

Temperature (°C)	Treatment	N	Days past time of first feeding 1	2	3	4	5	6	7
18	Starved	25	100	100	100	100	92	32	0
	Fed	25	100	100	100	100	96	92	92
20	Starved	25	92	76	72	48	8	4	0
	Fed	25	88	84	84	84	72	68	68
22	Starved	20	100	100	80	75	0		
	Fed	20	100	100	100	100	100		
24	Starved	25	56	40	40	4	0		
	Fed	25	96	96	96	96	96		

feeding or high mortalities will occur; whereas at 18°C they can survive without food for 5 d without incurring high mortalities (Table 3). The gulf menhaden's response to starvation in relation to temperature is comparable to numerous temperate zone, pelagic fish larvae (McGurk 1984).

In conclusion, although temperature is an important factor in controlling the development of marine fish larvae (Blaxter 1970), we observe that temperature was not a determinant of size at hatching, size at first feeding, and yolk volume remaining at first feeding. These data suggest that age is not a good correlate of these developmental events. On the other hand, temperature had an effect on the rate of yolk utilization, the time between hatching and exogenous feeding, and the ability of larvae to withstand the deprivation of food.

Our observations, although limited by a lack of rigorous statistical testing, suggest that, relative to gulf menhaden, Atlantic menhaden produced larger eggs, were larger at hatching, were larger and younger at time of first feeding, and appeared to maintain a larger size throughout the early larval period. We tried to interpret these differences in the context of their entire life history. Relative to gulf menhaden, Atlantic menhaden exhibit life history traits (later maturity, longer life, and more reproductive years) that may be adapted to a more fluctuating environment producing more reproductive uncertainty (Murphy 1968; Stearns 1976). This information suggests to us that the subtle differences we observed may indicate a fine tuning of reproductive strategies that allow these menhadens to persist in their particular environments. A more rigorous comparative study is required before we can understand how menhaden life history characteristics are adapted to their particular environments. Such a study is presently underway by the senior author.

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Literature Cited

BLAXTER, J. H. S.
1970. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 178-252. Acad. Press, Inc. N.Y.

BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons., Cons. Int. Explor. Mer 28:211-240.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20: 1-223.

CHRISTMAS, J. Y., AND R. S. WALLER.
1975. Location and time of menhaden spawning in the Gulf of Mexico. Gulf Coast Res. Lab., Ocean Springs, MS, 20 p.

HETTLER, W. F.
1981. Spawning and rearing Atlantic menhaden. Prog. Fish-Cult. 43:80-84.
1983. Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. Prog. Fish-Cult. 45:45-48.
1984. Description of eggs, larvae, and early juveniles of gulf menhaden, *Brevoortia patronus*, and comparisons with Atlantic menhaden, *B. tyrannus*, and yellowfin menhaden, *B. smithi*. Fish. Bull., U.S. 82:85-95.

HIGHAM, J. R., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63:255-271.

HOUDE, E. D., AND P. L. FORE.
1973. Guide to the identity of eggs and larvae of some Gulf of Mexico clupeid fishes. Fla. Dep. Nat. Resour., Mar. Res. Lab., Leafl. Ser. 4(23):1-14.

JONES, P. W., F. D. MARTIN, AND J. D. HARDY, JR.
1978. Development of fishes of the Mid-Atlantic Bight. Vol. 1, Acipensaridae through Ictaluridae. U.S. Fish. Wildl. Serv., Biol. Serv. Program FWS/OBS-78/12, 314 p.

LEWIS, R. M., AND C. M. ROITHMAYR.
1981. Spawning and sexual maturity of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 78:947-951.
MCGURK, W. D.
1984. Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. Mar. Biol. 84:13-26.
MURPHY, G. I.
1968. Pattern in life history and the environment. Am. Nat. 102:391-403.
NICHOLSON, W. R.
1975. Age and size composition of the Atlantic menhaden, *Brevoortia tyrannus*, purse seine catch, 1963-71, with a brief discussion of the fishery. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-684, 28 p.
1978. Movements and population structure of Atlantic menhaden indicated by tag returns. Estuaries 1:141-150.
REINTJES, J.
1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv., Circ. 320, 30 p.
STEARNS, S. C.
1976. Life-history tactics: a review of the ideas. Q. Rev. Biol. 51:3-47.

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SEASONALITY OF BLUE MUSSEL, *MYTILUS EDULIS* L., LARVAE IN THE DAMARISCOTTA RIVER ESTUARY, MAINE, 1969-77[1]

The spawning of the blue mussel, *Mytilus edulis* L., has been the subject of many studies (see Bayne 1976 for partial review). In an early paper Field (1922) reported that gametogenesis and spawning were influenced by water temperature, though he provided no data. Chipperfield (1953) found that mussels spawn over a specific range of water temperature (9.5°-12.5°C). In addition, Chipperfield noted that the rate of temperature change prior to spawning influences intensity. Other investigators have found that mussels spawn over a specific temperature range, which may vary among locales (Engle and Loosanoff 1944; Stubbings 1954; Baird 1966; Bohle 1971; Rasmussen 1973; Jorgensen 1981; Kautsky 1982).

Seed (1975) summarized reproduction in European mussel populations and found that spawning in *M. edulis* varies with latitude, occurring earlier in warm waters and progressively later in cooler, northern waters. However, Newell et al. (1982) reported no latitudinal variation of spawning among mussel populations along the northwestern Atlantic coast. Such geographic variation has been attributed to the existence of physiological races (Stauber 1950; Loosanoff and Nomejko 1951). Newell et al. (1982) and Fell and Belsamo (1985) also found that mussel populations at the same latitude in Long Island Sound spawn at different temperatures and times of the year. They surmised that food availability, rather than temperature, dictates when spawning occurs.

Factors which are important in the timing and intensity of spawning can be determined by monitoring spawning activity. This may be achieved directly, by examination of gonad development in seasonally collected samples, or indirectly, by observing the presence or absence of *M. edulis* larvae in plankton samples (Chipperfield 1953). While the direct method is preferable, the indirect method does allow one to use long-term plankton records. These provide an estimate of the variation in both the timing and intensity of spawning. Since the source of the larvae is not certain, some caution should be used in the interpretation of the results (Seed 1975).

An 8-yr plankton record of *Mytilus* larval abundance presents an unusual opportunity to observe long-term variability in spawning and larval occurrence. Specifically, the data were examined with the following goals:

1) Determination of the initiation and the duration of the spawning season and degree of temporal variation between years;
2) Determination of the variation in larval abundances within and between seasons;
3) Examination of the possible correlation of environmental variables (temperature, phytoplankton abundance, degree days, calendar date, and lunar cycles) with spawning activity.

Materials and Methods

The study site was the Damariscotta River estuary (Fig. 1), a narrow embayment, 29 km long, which receives a limited amount of freshwater. The estu-

[1]Contribution No. 183, Ira C. Darling Center, University of Maine, Orono, ME.

arine portion has a MLW (mean low water) volume of 123.4×10^6 m^3, a tidal volume of 56.2×10^6 m^3, and a mean summer flushing time of 4-5 wk (McAlice 1977). The estuary is stratified near its head but approaches a well-mixed condition further seaward. Tides are semi-diurnal with a mean range of 2.7 m and a tidal excursion of about 2.8 km (Lee and McAlice 1979).

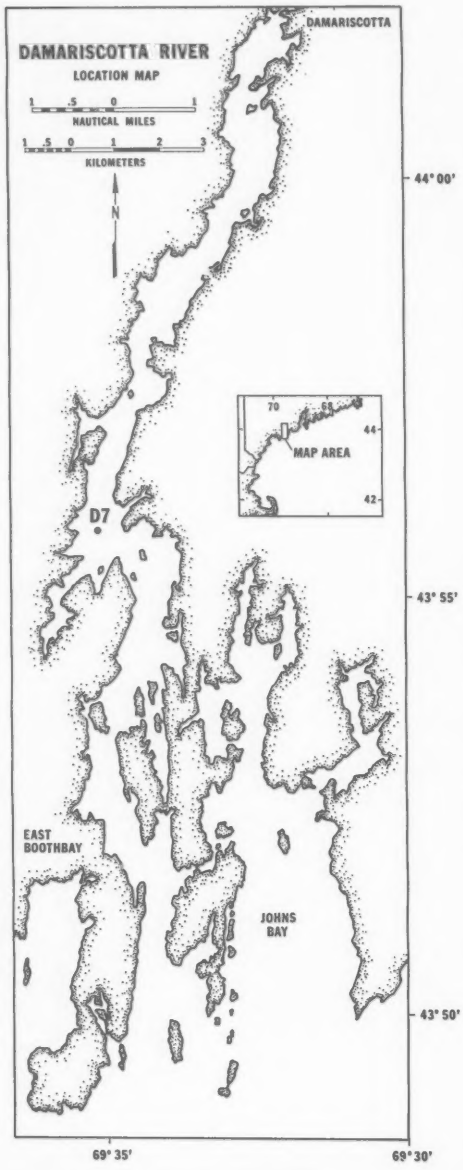

FIGURE 1.—Location map.

Monthly plankton samples were collected during daylight at station D7 (Fig. 1) from October 1969 to June 1970 and then biweekly until September 1977. Plankton tows were 10-15 min oblique hauls with #20 mesh (76 μm) nets of 0.5 m mouth diameter equipped with centrally mounted flowmeters. Maximum depths of tows were 10-15 m (4-5 m above the bottom). Boat speed was 1-2 m s^{-1}. Samples were immediately fixed in 4% buffered Formalin[2].

Laboratory subsampling followed the method recommended by Frolander (1968). The concentrated plankton was diluted to a known volume, thoroughly stirred, and a 1 mL aliquot removed with a Stempel pipette. Initial counts on samples taken from June 1974 to September 1977 did not distinguish among taxa of larval bivalves. We therefore took an additional subsample, determined the percentage of *Mytilus* in 50 bivalve larvae, and multiplied this by the total veliger abundance to obtain *Mytilus* densities for each sampling period.

Several key publications (Loosanoff et al. 1966; Chanley and Andrews 1971; DeScweinitz and Lutz 1976; Lutz and Hidu 1979) containing photomicrographs and descriptions were used to identify *Mytilus edulis* larvae. The differentiation of *Mytilus edulis* larvae from other mytilid larvae (*Modiolus modiolus* and *Geukensia demissa*) at the straight hinge stage was achieved by comparing the length of the hinge line as well as total shell length and height. The early and late umbo larvae of *Geukensia* were easily distinguishable by their elongated appearance; *Mytilus* larvae tended to be less elongate, though pointed anteriorly (Chanley and Andrews 1971). The differentiation of *Modiolus modiolus* larvae and *Mytilus edulis* larvae was based mainly on the characteristics described by DeSchweinitz and Lutz (1976); hinge line lengths, total shell length in the 95-105 μm range, shell shape of umbo stage larvae, presence of an eye spot in specimens <270 μm, and the presence of a functional foot in larvae <295 μm. Further positive identification of late stage *Mytilus* larvae was achieved by examining the hinge teeth of disarticulated valves (Lutz and Hidu 1979).

Spawning dates were estimated by subtracting the approximate age of the larvae from the sampling

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

date. Larval age was estimated using photomicrographs of larvae of known age and size for comparison, available in Chanley and Andrews (1971). The initial occurrence of larvae in each year was dominated by early straight hinge larvae. The spawning season was defined by larval abundances >10 m^{-3}. This level was chosen arbitrarily to distinguish major spawning from occasional low larval abundances (<10 m^{-3}).

Environmental variables that were examined for correlations with the initiation of spawning and larval abundance included water temperature, phytoplankton abundance, degree days, calendar date, and lunar cycles. Water temperatures were taken concurrently with the plankton samples. Phytoplankton abundances from July 1974 to August 1977 were available for the Damariscotta River (McAlice unpubl. data). Data from the neighboring Sheepscot River estuary (McAlice and Denniston[3]) were substituted for the period October 1969 to June 1974. The decision to use the Sheepscot data was based on the highly significant Spearman's rank correlation (Zar 1984) ($r = 0.67$, $P < 0.001$) between the Damariscotta and Sheepscot phytoplankton abundances from July 1974 to August 1977. Degree days were calculated in the manner described by Thiesen (1973). For each year, degree days were summed from the time of peak larval abundance the previous year to the initiation of spawning. Lunar cycle information was obtained from tide tables published by NOAA (1969-76).

Results

Examination of the age and abundance of mussel larvae from December 1969 to September 1977 indicated that spawning began in late May or early June when temperatures reached 10°-12.5°C (Fig. 2). The average date when spawning began was 4 June, with a standard deviation of approximately 7 d. The average number of degree days prior to spawning was 2,853, with a standard deviation of 368. No significant relationship was found between degree days and commencement of spawning or degree days and maximum larval abundances.

Commencement of spawning may be related to the time of spring tides (Table 1). In 7 of the 8 yr examined, spawning began within 5 d, before and after, a spring tide. On four occasions spawning commenced within 2 d of a spring tide. Spawning, once initiated, probably continued throughout the summer as indicated by the persistence of early stage mussel larvae. Spawning appeared to cease as temperatures fell to 9°-14°C in September and October (Fig. 2), when only late stage larvae were present. Maximal larval abundances were observed in mid- to late June, shortly after spawning began. At this time, straight hinge larvae, <6 d old, were dominant. Maximum values for the period 1970-75 ranged from 787 larvae m^{-3} to 5,400 larvae m^{-3}. In 1976 and 1977, maximum abundances were an order of magnitude larger (3.16×10^4 m^{-3} and 6.09×10^4 m^{-3}, respectively). Following the peaks in June, larval densities generally declined through 1 to 3 successively smaller peaks (Fig. 2).

Mussel larvae appeared well after phytoplankton abundances had begun to increase from low winter values to generally high summer values (Fig. 3). Larvae usually disappeared before phytoplankton abundances fell to typically low winter levels.

In addition to the larvae of *Mytilus edulis*, those of *Anomia simplex*, *Geukensia demissa*, *Modiolus modiolus*, and what was probably a complex of *Mya arenaria*, *Hiatella arctica*, and possibly *Sphenia sincera* (Hanks and Packer 1985) larvae were also identified. *Amonia simplex* occurred most commonly from September through December, though never in great numbers. The *Mya-Hiatella-Sphenia* group was often very abundant, and occurred from early May through September. *Geukensia* and *Modiolus* were never common.

TABLE 1.—Estimated dates and temperatures of the initiation and cessation of spawning for *Mytilus edulis* in the Damariscotta River estuary, and dates of nearest spring tides, 1970-77.

Year	Estimated date and (°C) when spawning began	Estimated date and (°C) when spawning ended	Date of nearest spring tide
1970	2 June (10.0°-13.2°C)	2 Oct. (14.6°-13.9°C)	June 4
1971	8 June (10.2°-12.2°C)	18 Oct. (14.3°-12.8°C)	June 9
1972	16 June (10.5°-12.1°C)	20 Oct. (13.1°-9.0°C)	June 11
1973	12 June (10.0°-14.0°C)	10 Oct. (12.7°-11.0°C)	June 15
1974	12 June (10.7°-12.3°C)	8 Oct. (12.4°-9.1°C)	June 4
1975	27 May (10.3°-12.5°C)	24 Sept. (16.9°-13.7°C)	May 25
1976	24 May (10.1°-12.8°C)	22 Oct. (14.6°-11.0°C)	May 29
1977	2 June (9.3°-10.2°C)	—	June 1

Discussion

A temperature threshold for spawning was indicated by the appearance of *Mytilus* larvae when water temperatures exceeded 10°-12.5°C and the subsequent disappearance of larvae when temperatures fell below 9°-14°C. A number of studies have reported the initiation of spawning in *Mytilus edulis*

[3]McAlice, B. J., and F. D. Denniston. Dominance and diversity of Sheepscot River estuary phytoplankton. Manuscr. in prep. Ira C. Darling Center, University of Maine, Walpole, ME 04573.

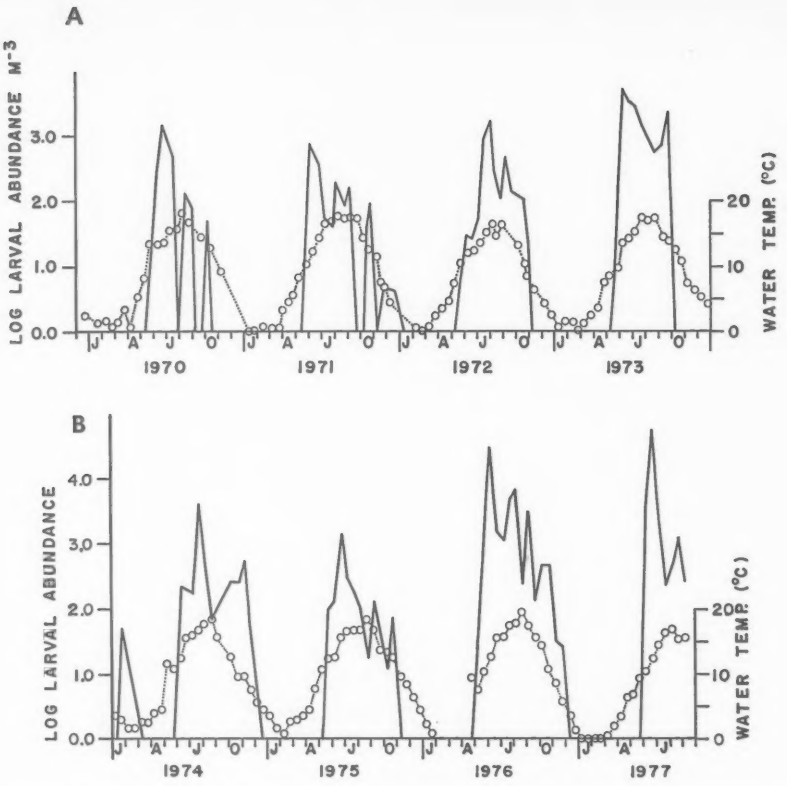

FIGURE 2.—Abundance of *Mytilus edulis* larvae (solid line) and water temperature (broken line) at station D7: A) 1969-73; B) 1974-77.

at temperatures of 10°-13°C or higher while few studies have reported spawning at lower temperatures (Table 2), which also suggests a thermal threshold for spawning. The significance of this threshold may be linked to gametogenesis. Bayne (1965) found that mussels with fully developed gametes would not spawn when held at 5°C under high food concentrations. However, if temperatures were raised to 12°-14°C, gametes matured and spawning ensued. Similarly, Sastry (1968) found that in the bay scallop, *Aequipecten irradians*, oogonia and spermatozoa formed at 15°C and 20°C, but that temperatures higher than 20°C were necessary for oocytes to reach a fertilizable stage. Therefore, the apparent correlation between a particular temperature and the initiation of spawning may actually reflect the maturation of gametes followed by induction of spawning by any of a number of stimuli. Given the predictable rise in temperature each spring, this may explain the initiation of spawning at approximately the same time each year.

Use of degree days to predict the time of spawning does not appear to be useful. This is due to a very regular pattern of rising and falling water temperatures each year. As a result, the sum of degree days between spawning periods conveyed no more information than did elapsed time. Newell et al. (1982) arrived at a similar conclusion for mussel populations in Long Island Sound. They found that one Long Island Sound mussel population spawned 3 mo later than another, despite nearly identical temperature conditions, difference in degree days due solely to a difference in elapsed calendar days. Bayne (1975), however, did find a relationship between rate of gametogenesis and degree days, but not calendar days.

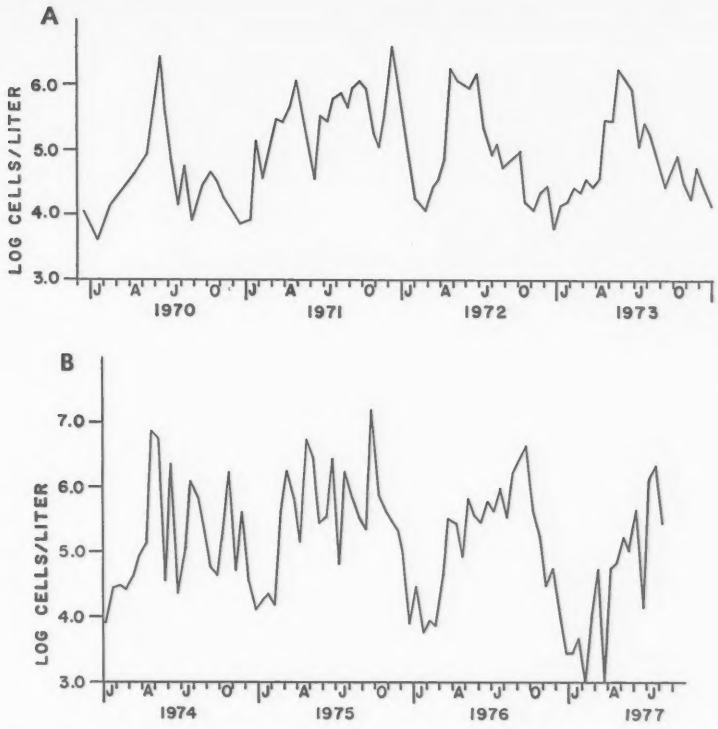

FIGURE 3.—Abundance of phytoplankton in the lower Sheepscot River estuary: A) 1969-73; B) January 1974-June 1974 and at station D7, July 1974-August 1977.

TABLE 2.—Reported spawning temperatures and periods of *Mytilus edulis*.

Location	Temperatures (°C)	Major spawning period	Reference
Europe			
Norway	8	early May	Bohle 1971
Denmark	7-16	May	Jorgensen 1981
England	9.5-12.5	May	Chipperfield 1953
Sweden	12	mid-May-early June	Kautsky 1982
England	13	early May	Baird 1966
Denmark	13-14	May-June	Rasmussen 1973
United States			
Damariscotta River, ME	10-13	late May-mid-June	This study
Milford, CT	15-16	May	Engle and Loosanoff 1944
Branford, CT	14-16	late May-early June	Fell and Balsimo 1985
Stony Brook, NY	11-15	late April-early June	Newell et al. 1982
Shinnecock, NY	16-22	August-October	Newell et al. 1982

Spawning in response to lunar cycles is also a possibility. Korringa (1947) noted that the European oyster, *Ostrea edulis*, spawns around the period of spring tides and attributed this to increased hydrostatic pressure. Chipperfield (1953) also observed *O. edulis* at several sites in Great Britain shortly after

the occurrence of a spring tide. In our study, spawning began around the time of spring tides, but induction of spawning by hydrostatic pressure has not been reported in mussels. Alternatively, spawning may be induced by other factors associated with spring tides, such as increased temperature fluctuations, air exposure, and water movement. Temperature fluctuations have been shown to induce laboratory spawning in *Mytilus edulis* (Bayne 1976).

While a temperature threshold is suggested, time of year may also be important as indicated by the spawning periods in Table 2. Of the 10 studies examined, all but one reported the initiation of spawning from May to June. Aside from temperature, the initiation of spawning may be influenced by another cyclic phenomena such as photoperiod. Light and photoperiod in particular have been shown to affect the timing of reproduction in a number of marine invertebrates (Segal 1970). While adult mussels are sensitive to changes in light intensity (Bayne et al. 1976), the ability to detect changing photoperiod has not been demonstrated. The results of this study have been attributed to annual temperature cycles, but until light response of mussels is more fully examined photoperiod cannot be ruled out.

Variations in larval abundance from year to year do not appear to be linked to temperature, nor to availability of food energy. Kautsky (1982) reported that Baltic Sea mussel populations were limited to one major spawning by reduced food availability during the remainder of the year. Similarly, Thompson (1979) attributed annual variation in reproductive condition and fecundity of mussels along the coast of Nova Scotia to annual variations in food supply. Bayne (1975) noted that while poor nutrition does not significantly alter the timing of gametogenesis, it can result in resorption of gametes prior to spawning. Newell et al. (1982) suggested that the cycle of food availability could affect both the nutrient storage cycle and the timing of gametogenic events, including spawning. In every year of our study the spring augmentation of phytoplankton was well under way by March or April, with densities $>10^5$ cells l^{-1}. Significant numbers of mussel larvae were first detected between late May and early June. Thus, it appears that food is not limiting to either adult or larval mussel populations in our area. Our phytoplankton data, however, do not include the smaller naked nanoplankton which, together with particulate organic matter, could account for more than half of the available energy in the Damariscotta River (Incze 1979). This fraction would be a better index of food available to mussel larvae and should be included in studies attempting to link abundance or setting success of larvae to their food supply.

Onset of spawning in Damariscotta River mussel populations is predictable from year to year. It occurs when water temperature exceeds 10°-12.5°C, and near the spring tide portion of the neap-spring cycle. Food does not appear to be limiting to either gametogenesis or the development of larvae.

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Literature Cited

BAIRD, R. H.
1966. Factors affecting the growth and condition of mussels (*Mytilus edulis* L.). Fish. Invest., Lond., Ser. II, 25:1-33.

BAYNE, B. L.
1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1-47.
1975. Reproduction in bivalve molluscs under environmental stress. *In* F. J. Vernberg (editor), Physiological ecology of estuarine organisms, p. 259-277. Univ. South Carolina Press.
1976. The biology of mussel larvae. *In* B. L. Bayne (editor), Marine mussels: their ecology and physiology, p. 81-120. Cambridge Univ. Press, N.Y.

BAYNE, B. L., J. WIDDOWS, AND R. J. THOMPSON.
1976. Physiology II. *In* B. L. Bayne (editor), Marine mussels: their ecology and physiology, p. 207-260. Cambridge Univ. Press, N.Y.

BOHLE, B.
1971. Settlement of mussel larvae *Mytilus edulis* on suspended collectors in Norwegian waters. 4th Eur. Mar. Biol. Symp., p. 63-69.

CHANLEY, P., AND J. D. ANDREWS.
1971. Aids for identification of bivalve larvae of Virginia. Malacologia 11:45-119.

CHIPPERFIELD, P. N. J.
1953. Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. J. Mar. Biol. Assoc. U.K. 32:449-476.

DESCHWEINITZ, E. H., AND R. A. LUTZ.
1976. Larval development of the northern horse mussel, *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* (L.) as an aid in planktonic identification. Biol. Bull. (Woods Hole) 150:348-360.

ENGLE, J. B., AND V. L. LOOSANOFF.
1944. On season of attachment of larvae of *Mytilus edulis*. Ecology 25:433-440.

FELL, P. E., AND A. M. BALSAMO.
1985. Recruitment of *Mytilus edulis* L. in the Thames estuary, with evidence of differences in the time of maximal settling along the Connecticut shore. Estuaries 8:68-75.

FIELD, I. A.
1922. Biology and economic value of the sea mussel *Mytilus*

edulis. Fish. Bull., U.S. 38:127-260.

FROLANDER, H. F.
1968. Statistical variation in zooplankton numbers from subsampling with a Stempel pipette. J. Water Pollut. Control Fed. 40:R82-R88.

HANKS, R. W., AND D. B. PACKER.
1985. A new species of *Sphenia* (*Bivalvia:Myidae*) from the Gulf of Maine. Veliger 27:320-330.

INCZE, L. S.
1979. Relationships between environmental temperatures, seston, and the growth and survival of *Mytilus edulis*, L. in a north temperate estuary. M.S. Thesis, Univ. Maine, Orono.

JORGENSON, C. B.
1981. Mortality, growth and grazing impact of a cohort of bivalve larvae, *Mytilus edulis*. (L.). Ophelia 20:185-192.

KAUTSKY, N.
1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. Mar. Biol. (Berl.) 58:143-160.

KORRIGA, P.
1947. Relations between the moon and periodicity in the breeding of marine animals. Ecol. Monogr. 17:347-381.

LEE, W. Y., AND B. J. MCALICE.
1979. Sampling variability of marine zooplankton in a tidal estuary. Estuarine Coastal Mar. Sci. 8:565-582.

LOOSANOFF, V. L., H. C. DAVIS, AND P. E. CHANLEY.
1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia 4:351-435.

LOOSANOFF, V. L., AND C. A. NOMEJKO.
1951. Existence of physiologically different races of oysters, *Crassostrea virginica*. Biol. Bull. (Woods Hole) 101:151-156.

LUTZ, R. A., AND H. HIDU.
1979. Hinge morphogenesis in the shells of larval and early post-larval mussels (*Mytilus edulis* and *Modiolus modiolus* L.). J. Mar. Biol. Assoc. U.K. 59:111-121.

MCALICE, B. J.
1977. A preliminary oceanographic survey of the Damariscotta River estuary, Lincoln County, Maine. Maine Sea Grant Tech. Rep. 13, 27 p.

NEWELL, R. I. E., T. J. HILBISH, R. K. KOEHN, AND C. J. NEWELL.
1982. Temporal variation in the reproductive cycle of *Mytilus edulis* L. (*Bivalvia, Mytilidae*) from localities on the east coast of the United States. Biol. Bull. (Woods Hole) 162: 299-310.

NOAA.
1969-1976. Tide Tables: East Coast of North and South America, including Greenland. Tide Tables Natl. Ocean Surv. (U.S.) 1969-1976.

RASMUSSEN, E.
1973. Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. Ophelia 11:1-495.

SASTRY, A. N.
1968. The relationships among food, temperature and gonad development of the bay scallop, *Aequipecten irradians* Lamarck. Physiol. Zool. 41:44-53.

SEED, R.
1975. Reproduction in *Mytilus* (*Mollusca:Bivalvia*) in European waters. Publ. Stn. Zool. Napoli 39(suppl. 1):317-334.

SEGAL, E.
1970. Light, animals, invertebrates. *In* O. Kinne (editor), Marine ecology, Vol. I, Part I, p. 159-211. Wiley-Interscience, N.Y.

STAUBER, L. A.
1950. The problem of physiological species with special reference to oysters and oyster drills. Ecology 31:109-118.

STUBBINGS, H. G.
1954. The biology of the common mussel in relation to fouling problems. Research 7:222-229.

THEISEN, B. F.
1973. The growth of *Mytilus edulis* L. (*Bivalvia*) from Disko and Thule district, Greenland. Ophelia 12:59-77.

THOMPSON, R. J.
1979. Fecundity and reproductive effort in the blue mussel (*Mytilus edulis*), the sea urchin (*Stronglyocentrotus droebachiensis*) and the snow crab (*Chionocetes opilio*) from populations in Nova Scotia and Newfoundland. J. Fish. Res. Board Can. 36:955-964.

ZAR, J. H.
1984. *Biostatistical analysis*. 2d ed. Prentice-Hall, Englewood Cliffs, N.J.

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INDEX

Fishery Bulletin Vol. 84, No. 1-4

"The abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfolk Canyon area," by Robert W. Middleton and John A. Musick 35

"Abundance, size, and sex ratio of adult sea-run sea lampreys, *Petromyzon marinus*, in the Connecticut River," by Kathleen Stier and Boyd Kynard 476

"Age and growth of the marine catfish, *Netuma barba* (Siluriformes, Ariidae), in the estuary of the Patos Lagoon (Brasil)," by Enir Girondi Reis 679

"Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*," by Richard H. Parrish, Donna L. Mallicoate, and Richard A. Klingbeil 503

Aging studies
larval fish 91
sailfish, Atlantic 493

AHRENHOLZ, DEAN W.—see NELSON and AHRENHOLZ

Albacore
chromosomal analysis 469

Ammodytes americanus—see Eel, sand

Ammodytes hexapterus—see Sand lance

Ampelisca agassizi—see Amphipods, gammaridean

Amphipods, benthic
parasites of 204, 605

"Anatomical trauma to sponge-coral reef fishes captured by trawling and angling," by S. Gordon Rogers, Hiram T. Langston, and Timothy E. Targett 697

Anchovy, northern
fecundity and spawning 503
drift in the California Current 585
life-stage-specific instantaneous mortality rates 395
spawning in San Francisco Bay 879
vulnerability to predation 859

"An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas," by Jeffrey J. Polovina and Stephen Ralston .. 759

Anglerfish, lophiid
early development 429

Angling
trauma to sponge-coral reef fishes 697

Anguilla rostrata—see Eel, American

"Annual production of eviscerated body weight, fat, and gonads of Pacific herring, *Clupea harengus pallasi*, near Auke Bay, southeastern Alaska," by Jay C. Quast 705

Anoplopoma fimbria—see Sablefish

Anthozoans
ecology of Ceriantharia from Cape Hatteras to Nova Scotia 625

Arctica islandica—see Quahog, ocean

"Arrival of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska," by Michael A. Bigg 383

Ascarophis sp.
parasites in American lobster 197

"Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp, *Heterocarpus laevigatus*, in Hawaii," by Murray D. Dailey and Stephen Ralston 915

Atheresthes evermanni—see Flounder, Kamchatka

Atheresthes stomias—see Flounder, arrowtooth

ATKINSON, C. ALLEN, "Discrete-time difference model for simulating interacting fish population dynamics"... 535

Backdown
dolphin-releasing procedure 27

Balaenoptera edeni—see Whale, Bryde

Balaenoptera physalus—see Whale, finback

BALTZ, DONALD M.—see MOYLE et al.

BARBER, RICHARD T.—see FORWARD et al.

BARLOW, J.—see MYRICK et al.
—see REILLY and BARLOW

Bass, black sea
anatomical trauma from angling 697
contributions to life history 723

Bass, striped
feeding below a hydroelectric dam 220
survival and growth 905

BAYER, RANGE D., "Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Niño".. 279

BEACHAM, TERRY D., "Type, quantity, and size of food of Pacific salmon (*Oncorhynchus*) in the Strait of Juan de Fuca, British Columbia" 77

BIANCHINI, MARCO L.—see SORENSEN et al.

BIGG, MICHAEL A., "Arrival of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska" 383

BIGG, MICHAEL A.—see PEREZ and BIGG

BODKIN, JAMES LEE, "Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California"..... 799

BOEHM, PAUL D.—see STEIMLE et al.

BONNELL, MICHAEL L.—see DOHL et al.

Boston
Ex-vessel price in New England fishing industry 437

BOTSFORD, LOUIS W.—see SYKES and BOTSFORD

Bottomfish
affect of hypoxia on abundance and distribution..... 19

Brevoortia patronus—see Menhaden, gulf

Brevoortia tyrannus—see Menhaden, Atlantic

Briarosaccus callosus—see Rhizocephalan

BRUNO, RALPH A.—see STEIMLE et al.

BRUSHER, HAROLD A.—see FINUCANE et al.

BURCH, RAYMOND, K.—see UCHIYAMA et al.

Calanus pacificus
abundance, chemical composition, distribution, and size 157
California Current 157

California Cooperative Oceanic Fisheries Investigation
northern anchovy drift studies 587

California Current
Calanus pacificus 157
northern anchovy..... 585

Callorhinus ursinus—see Seal, northern fur

CAREY, ANDREW G., JR.—see TESTER and CAREY

"Cartilage and bone development in scombroid fishes," by Thomas Potthoff, Sharon Kelley, and Joaquin C. Javech.. 647

Catfish, sea
age and growth in Patos Lagoon, Brasil 679

Centrapristis striata—see Bass, black sea

Ceriantharia—see Anthozoans

"Cetacean high-use habitats of the northeast United States continental shelf," by Robert D. Kenney and Howard E. Winn..... 345

Cetaceans
high-use habitats 345
sighted by CETAP aerial and POP surveys..... 349

CETAP
aerial surveys..... 345

"Chinook salmon, *Oncorhynchus tshawytscha*, spawning escapement based on multiple mark-recapture of carcasses," by Stephen D. Sykes and Louis W. Botsford..... 261

Chionoecetes tanneri—see Crab, spider

Chlorophyll
sea surface concentration in the tropical Pacific..... 687

"Chromosomal analysis of albacore, *Thunnus alalunga*, and yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*, tuna," by F. J. Ratty, Y. C. Song, and R. M. Laurs..... 469

Ciliates
parasites of benthic amphipods 204

Clam, soft shell
description of poecilostomatoid copepods 227
occurrence of epizootic sarcoma in Chesapeake Bay.. 851

Clupea harengus pallasi—see Herring, Pacific

Cod
ex-vessel price in New England fishing industry 437

CODY, TERRY J., and BILLY E. FULS, "Comparison of catches in 4.3 m and 12.2 m shrimp trawls in the Gulf of Mexico" 981

Coelorinchus c. carminatus
abundance and distribution in Norfolk Canyon 37

COLLETTE, BRUCE B., "Resilience of the fish assemblage in New England tidepools" 200

COLLINS, L. ALAN—see FINUCANE et al.

"Community studies in seagrass meadows: A comparison of two methods for sampling macroinvertebrates and fishes," by Kenneth M. Leber and Holly S. Greening .. 443

"Comparison of catches in 4.3 m and 12.2 m shrimp trawls in the Gulf of Mexico," by Terry J. Cody and Billy E. Fuls 981

"Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions," by William H. Lenarz and Tina Wyllie Echeverria..... 743

Connecticut River
spawning migration of sea lampreys..... 749

"Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States," by Charles A. Wenner, William A. Roumillat, and C. Wayne Waltz 723

COOPER, RICHARD A.—see SHEPARD et al.

"Copepodids and adults of *Leptinogaster major* (Williams, 1907), a poecilostomatoid copepod living in *Mya arenaria* L. and other marine bivalve mollusks," by Arthur G. Humes 227

Copepods
size and chemical composition 165

Copepods, poecilostomatoid
Leptinogaster major living in mollusks 227
taxonomic history 227

Coryphaena equiselis—see Dolphin, pompano

Coryphaena hippurus—see Dolphin (fish)

Coryphaenoides armatus
abundance and distribution in Norfolk Canyon 51

Coryphaenoides carapinus
abundance and distribution in Norfolk Canyon 51

Coryphaenoides rupestris
abundance and distribution in Norfolk Canyon 48

COX, JAMES L.—see WILLASON et al.

Crab, blue king
Rhizocephalan infection 177

Crab, golden king
distribution and reproductive biology in eastern Bering Sea 571

Crab, king
comparison of blue and golden king crabs 327

Crab, spider
instar identification 973
life history 973

Culture studies
squid, market 771

CUMMINGS, WILLIAM C., PAUL O. THOMPSON, and SAMUEL J. HA, "Sounds from Bryde, *Balaenoptera edeni*, and finback, *B. physalus*, whales in the Gulf of California" 359

DAILEY, MURRAY D., and STEPHEN RALSTON, "Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp, *Heterocarpus laevigatus*, in Hawaii" 915

Dams, hydroelectric
striped bass feeding area 220

DANDONNEAU, YVES, "Monitoring the sea surface chlorophyll concentration in the tropical Pacific: consequences of the 1982-83 El Niño" 687

DANIELS, ROBERT A.—see MOYLE et al.

DEAN, JOHN M.—see PRINCE et al.

Delphinus delphis—see Dolphin, common

de MENDIOLA, BLANCA ROJAS—see FORWARD et al.

"Determining age of larval fish with the otolith increment technique," by Cynthia Jones 91

"Development and evaluation of methodologies for assessing and monitoring the abundance of widow rockfish, *Sebastes entomelas*," by Mark E. Wilkins 287

Developmental studies
scombroid fishes 647

"Diel foraging activity of American eels, *Anguilla rostrata* (LeSueur), in a Rhode Island estuary," by Peter W. Sorensen, Marco L. Bianchini, and Howard E. Winn .. 746

"Diet of northern fur seals, *Callorhinus ursinus*, off western North America," by Michael A. Perez and Michael A. Bigg 957

"Differentiation of *Prionotus carolinus* and *Prionotus evolans* eggs in Hereford Inlet estuary, southern New Jersey, using immunodiffusion," by Walter J. Keirans, Sidney S. Herman, and R. G. Malsberger 63

Dinoflagellates
swimming speed of *Gymnodinium splendens* 461
parasites of benthic amphipods 605

"Discrete-time difference model for simulating interacting fish population dynamics," by C. Allen Atkinson 535

Disease
epizootic sarcoma in soft shell clams 851

Dissolved oxygen concentration
effect on shrimp and bottomfish in Louisiana coastal waters 19

"Distribution and abundance of common dolphin, *Delphinus delphis*, in the Southern California Bight: a quantitative assessment based upon aerial transect data," by Thomas P. Dohl, Michael L. Bonnell, and R. Glenn Ford.. 333

"Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the eastern Bering Sea," by David A. Somerton and Robert S. Otto 571

"The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*," by P. Michael Payne, John R. Nicolas, Loretta O'Brien, and Kevin D. Powers 271

DITTY, JAMES G., "Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality" 935

DOHL, THOMAS P., MICHAEL L. BONNELL, and R. GLENN FORD, "Distribution and abundance of common dolphin, *Delphinus delphis*, in the Southern California Bight: a quantitative assessment based upon aerial transect data" 333

Dolphin, common
distribution and abundance in southern California ... 333

Dolphin (fish)
growth in Hawaiian waters by daily increments 186
stock structure in western central Atlantic 451

Dolphin, spotted
reproductive biology in eastern tropical Pacific..... 247

Dolphins
increase in population size 527
mortality
due to tuna purse seine fishery 27
in eastern tropical Pacific tuna fishery 559

"Early development of the Lophiid anglerfish, *Lophius gastrophysus*," by Yasunobu Matsuura and Nelson Takumi Yoneda 429

EARLY, GREG—see SELZER et al.

"Early life history of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*," by Allyn B. Powell and Germano Phonlor 991

ECHEVERRIA, TINA WYLLIE—see LENARZ and ECHEVERRIA

Echo integration
assessing widow rockfish abundance..... 287

"An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll," by Stephen Ralston, Reginald M. Gooding, and Gerald M. Ludwig..... 141

Ecology
anthozoans 625
bottom fish resource assessment at Johnston Atoll .. 141
community studies in seagrass meadows 443

"Ecology of Ceriantharia (Coelenterata, Anthozoa) of the northwest Atlantic from Cape Hatteras to Nova Scotia," by Andrew N. Shepard, Roger B. Theroux, Richard A. Cooper, and Joseph R. Uzmann 625

Economic studies
spiny lobster..... 69, 74

Ecosystems
fish population dynamic simulations 535

Eel, American
diel foraging activity..... 746

Eel, sand
relationship to humpback whale..... 271

"Effects of exposure and confinement on spiny lobsters, *Panulirus argus*, used as attractants in the Florida trap fishery," by John H. Hunt, William G. Lyons, and Frank S. Kennedy, Jr..... 69

"Effects of temperature on swimming speed of the dinoflagellate, *Gymnodinium splendens*," by Richard B. Forward, Jr., Blanca Rojas de Mendiola, and Richard T. Barber 460

El Niño
chlorophyll concentration in tropical Pacific 687
correlations of seabirds and salmon smolts 279
fat volume of yellowtail rockfish 743

Engraulis mordax—see Anchovy, northern

Euphausia pacifica..... 161

Euphausiids
distribution and abundance in California Current 161
invertebrate prey of Pacific salmon 77

"Ex-vessel price linkages in the New England fishing industry," by Dale Squires 437

FARLEY, C. A., S. V. OTTO, and C. L. REINISCH, "New occurrence of epizootic sarcoma in Chesapeake Bay soft shell clams, *Mya arenaria* 851

FAVUZZI, JC N—see WILLASON et al.

"Fecundity of northern shrimp, *Pandalus borealis*, (Crustacea, Decapoda) in areas of the Northwest Atlantic," by D. G. Parsons and G. E. Tucker 549

"Fecundity of the Pacific hake, *Merluccius productus*, spawning in Canadian waters," by J. C. Mason 209

FINUCANE, JOHN H., L. ALAN COLLINS, HAROLD A. BRUSHER, and CARL H. SALOMAN, "Reproductive biology of king mackerel, *Scomberomorus cavalla*, from the southeastern United States" 841

FIORELLI, PATRICIA M.—see SELZER et al.

"First record of the longfin mako, *Isurus paucus*, in the Gulf of Mexico," by Kristie Killam and Glenn Parsons.. 748

Fish
assemblages in kelp forests 799
resilience in New England tidepools 200

"Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California," by James Lee Bodkin .. 799

Fish population studies
food consumption estimates 827
simulating population dynamics 535

Fishery
crab, golden king..... 571
hypoxia in Louisiana coastal waters 19
management..... 697
menhaden, gulf 311
rockfish, commercial 409
spiny lobster, Florida 69
tuna purse seine and dolphin mortality 27
tuna, yellowfin 247, 559

Fishes
community studies in seagrass meadows 443
distribution and abundance in Suisan Marsh 105

Fishes, reef
trauma from trawling and angling 697

Fishing
ex-vessel price in New England fishing industries ... 437
multispecies intensive fishing experiment 423
shrimp
caridean 927
submersible versus handline 141

Fistulicola plicatus—see Tapeworm

Flounder
ex-vessel price linkages in New England 437

Flounder, arrowtooth
food habits in eastern Bering Sea 615
genetic confirmation of specific distinction 222

Flounder, Kamchatka
food habits in eastern Bering Sea 615
genetic confirmation 222

Flounder, yellowtail
statistical methods for estimating abundance 519

FOLKVORD, ARILD, and JOHN R. HUNTER, "Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes" 859

Food habits
bass, striped 220
fish consumption estimates 615
flounder 615, 827
hake, Pacific 947
salmon, Pacific 77
seal, northern fur 957

"Food habits and diet overlap of two congeneric species, *Atheresthes stomias* and *Atheresthes evermanni*, in the eastern Bering Sea," by M. S. Yang and P. A. Livingston.. 615

FORD, R. GLENN—see DOHL et al.

FORWARD, RICHARD B., JR., BLANCA de MENDIOLA, and RICHARD T. BARBER, "Effects of temperature on swimming speed of the dinoflagellate, *Gymnodinium splendens*" 460

FROST, KATHRYN J., and LLOYD F. LOWRY, "Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea" 192

FULS, BILLY E.—see CODY and FULS

Gammaridean amphipods 204

"Genetic confirmation of specific distinction of arrowtooth flounder, *Atheresthes stomias*, and Kamchatka flounder, *A. evermanni*," by Carol L. Ranck, Fred M. Utter, George B. Milner, and Gary B. Smith 222

Genetic studies
chromosomal analysis of tuna 469
specific distinction of flounder 222

Georges Bank
distribution of humpback whales 271

GIBSON, DARCY L.—see GRAHAM et al.

Gloucester
ex-vessel price in New England fishing industry 437

GOLDBERG, STEPHEN R.—see WEBER and GOLDBERG

GOODING, REGINALD M.—see RALSTON et al.

GRAHAM, JEFFREY B., RICHARD H. ROSENBLATT, and DARCY L. GIBSON, "Morphology and possible swimming mode of a yellowfin tuna, *Thunnus albacares*, lacking one pectoral fin" 463

GREENING, HOLLY S.—see LEBER and GREENING

Groupers
unexploited resources in the Marianas 759

GROVER, JILL J., and BORI L. OLLA, "Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*" 484

"Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle," by W. T. Yang, R. F. Hixon, P. E. Turk, M. E. Krejci, W. H. Hulet, and R. T. Hanlon 771

"Growth of dolphins, *Coryphaena hippurus*, and *C. equiselis*, in Hawaiian waters as determined by daily increments on otoliths," by James H. Uchiyama, Raymond K. Burch, and Syd A. Kraul, Jr. 186

Growth rates
anchovy, northern 503
bass, black sea 723
bass, striped 905
catfish, sea 679
dolphin fishes in Hawaiian waters 186
herring, Pacific 705
shrimp, caridean 915
squid, market 771

Gulf of California
sounds of Bryde and finback whales 359

Gulf of Maine
distribution of humpback whales 271

Gulf of Mexico
first record of longfin mako 748
ichthyoplankton 935

Gymnodinium splendens—see Dinoflagellate

HA, SAMUEL J.—see CUMMINGS et al.

Habitat studies
cetaceans of the northeast United States 345

Haddock
ex-vessel price in New England fishing industry 437

Hake, Pacific
fecundity in Canadian waters 209
stomach contents and food consumption 947

HANLON, R. T.—see YANG et al.

HARRIS, R. E., JR.—see VAN ENGEL et al.

Hatcheries
growth and survival of striped bass 905

HAWKES, CLAYTON R., THEODORE R. MEYERS, and THOMAS C. SHIRLEY, "Length-weight relationships of blue, *Paralithodes platypus*, and golden, *Lithodes aequispina*, king crabs parasitized by the rhizocephalan, *Briarosaccus callosus* Boschma" 327

HERBOLD, BRUCE—see MOYLE et al.

HERMAN, SIDNEY S.—see KEIRANS et al.

Herring, Pacific
annual production 705

Heterocarpus laevigatus—see Shrimp, caridean

Heterostichus rostratus—see Kelpfish, giant

Histology
starvation induced mortality 1

HIXON, R. F.—see YANG et al.

HOGANS, W. E., and P. C. F. HURLEY, "Variations in the morphology of *Fistulicola plicatus* Rudolphi (1802) (Cestoda: Pseudophyllidea) from the swordfish, *Xiphias gladius* L., in the northwest Atlantic Ocean" 754

HOHN, A. A.—see MYRICK et al.

Homarus americanus—see Lobster, American

HOUDE, EDWARD D., and LAWRENCE LUBBERS III, "Survival and growth of striped bass, *Morone saxatilis*, and *Morone* hybrid larvae: laboratory and pond enclosure experiments 905

HULET, W. H.—see YANG et al.

HUMES, ARTHUR G., "Copepodids and adults of *Leptinogaster major* (Williams, 1907), a poecilostomatoid copepod living in *Mya arenaria* L. and other marine bivalve mollusks" 227

HUNT, JOHN H., WILLIAM G. LYONS, and FRANK S. KENNEDY, JR., "Effects of exposure and confinement on spiny lobsters, *Panulirus argus*, used as attractants in the Florida trap fishery" 69

HUNTE, WAYNE—see OXENFORD and HUNTE

HUNTER, J. ROE, BEVERLY J. MACEWICZ, and JOHN R. SIBERT, "The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific" 895

HUNTER, JOHN R.—see FOLKVORD and HUNTER

HURLEY, P. C. F.—see HOGANS and HURLEY

Hybrids, bass striped
survival and growth 905

"Hypoxia in Louisiana coastal waters during 1983: implications for fisheries," by Maurice L. Renaud 19

"Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality," by James G. Ditty 935

Immunodiffusion
differentiation of *Prionotus* eggs 63

"An improved otter surface sampler," by J. C. Mason and A. C. Phillips 480

"Incidental dolphin mortality in the eastern tropical Pacific tuna fishery, 1973 through 1978," by Bruce E. Wahlen.. 559

"Incidental mortality of dolphins in the eastern tropical Pacific, 1959-72," by N. C. H. Lo and T. D. Smith 27

"Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus*," by Michael A. Perez and Elizabeth E. Mooney 371

"Instar identification and life history aspects of juvenile deepwater spider crabs, *Chionoecetes tanneri* Rathbun," by Patricia A. Tester and Andrew G. Carey, Jr. 973

"An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago," by Stephen Ralston 927

Istiophorus platypterus—see Sailfish, Atlantic

Isurus paucus—see Shark, longfin mako

JAVECH, JOAQUIN C.—see POTTHOFF et al.

JOHNSON, P. T., R. A. MacINTOSH, and D. A. SOMERTON, "Rhizocephalan infection in blue king crabs, *Paralithodes platypus*, from Olga Bay, Kodiak Island, Alaska" 177

JOHNSON, PHYLLIS T., "Parasites of benthic amphipods: ciliates" 204

JOHNSON, PHYLLIS T., "Parasites of benthic amphipods: dinoflagellates (Duboscquodinida: Syndinidae) ... 605

Johnston Atoll
resource assessment 141

Jolly-Seber
spawning escapement of chinook salmon 261

JONES, CYNTHIA, "Determining age of larval fish with the otolith increment technique" 91

Katsuwonus pelamis—see Tuna, skipjack

KEIRANS, WALTER J., SIDNEY S. HERMAN, and R. G. MALSBERGER, "Differentiation of *Prionotus carolinus* and *Prionotus evolans* eggs in Hereford Inlet estuary, southern New Jersey, using immunodiffusion".. 63

KELLEY, SHARON—see POTTHOFF et al.

Kelp, bull
fish assemblages in kelp forests 799

Kelp forests
fish assemblages 799

Kelp, giant
fish assemblages in kelp forests 799

Kelpfish, giant
life history and larval development 809

KENNEDY, FRANK S., JR.—see HUNT et al.

KENNEY, ROBERT D., and HOWARD E. WINN, "Cetacean high-use habitats of the northeast United States continental shelf" 345

KILLAM, KRISTIE, and GLENN PARSONS, "First record of the longfin mako, *Isurus paucus*, in the Gulf of Mexico" 748

KLINGBEIL, RICHARD A.—see PARRISH et al.

KRAUL, SYD A., JR.—see UCHIYAMA et al.

KREJCI, M. E.—see YANG et al.

KRYGIER, E. E., and W. G. PEARCY, "The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon" 119

KYNARD, BOYD—see STIER and KYNARD
—see WARNER and KYNARD

Lampreys, sea
abundance, size, and sex ratio 476
movement in the Connecticut River 749

LANGSTON, HIRAM T.—see ROGERS et al.

Larvae
anchovy, northern
in the California Current 585
instantaneous mortality rates 395
spawning and predation in San Francisco Bay 879
vulnerability of 859
anglerfish, lophiid
early development and comparison with other lophiid species 429
bass, striped
survival and growth 905
fish
age determination 91
kelpfish, giant 809
mackerel, jack 1
mussels, blue
spawning and seasonality 995
sablefish
starvation and prey size selection 484
scombroid
cartilage and bone development 647

LAURS, R. M.—see RATTY et al.

LEBER, KENNETH M., and HOLLY S. GREENING, "Community studies in seagrass meadows: A comparison of two methods for sampling macroinvertebrates and fishes" 443

LEE, DENNIS W.—see PRINCE et al.

LENARZ, WILLIAM H., and TINA WYLLIE ECHEVERRIA, "Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions" 743

"Length-weight relationships of blue, *Paralithodes platypus*, and golden, *Lithodes aequispina*, king crabs parasitized by the rhizocephalan, *Briarosaccus callosus* Boschma," by Clayton R. Hawkes, Theodore R. Meyers, and Thomas C. Shirley 327

Leptinogaster major—see Copepod, poecilostomatoid

Leslie model
dolphin population studies 527
fish population studies 535
variable catchability version 423

"Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard, 1854," by Carol A. Stepien 809

Life history studies
bass, black sea 723
crab, spider 973
kelpfish, giant 809
menhaden, Atlantic and gulf 991

Limanda ferruginea—see Flounder, yellowtail

Line intercept survey
assessing widow rockfish abundance 287

Line transect survey
assessing widow rockfish abundance 287

Literature review
daily deposition of otolith increments 91

Lithodes aequispina—see Crab, golden king

LIVINGSTON, P. A.—see YANG and LIVINGSTON

LO, NANCY C. H., "Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae" 395

LO, N. C. H., and T. D. SMITH, "Incidental mortality of dolphins in the eastern tropical Pacific, 1959-72" 27

Lobster, American
occurrence of parasites 197

Lobster, spiny
in Florida trap fishery 69

Loligo opalescens—see Squid, market

"Longevity and age validation of a tag-recaptured Atlantic sailfish, *Istiophorus platypterus*, using dorsal spines and otoliths," by Eric D. Prince, Dennis W. Lee, Charles A. Wilson, and John M. Dean 493

Lophius gastrophysus—see Anglerfish, lophiid

Louisiana
hypoxia in coastal waters 19

LOWRY, LLOYD F.—see FROST and LOWRY

LUBBERS, LAWRENCE III—see HOUDE and LUBBERS

LUDWIG, GERALD M.—see RALSTON et al.

LYONS, WILLIAM G.—see HUNT et al.

MACEWICZ, BEVERLY J.—see HUNTER et al.

MacINTOSH, R. A.—see JOHNSON et al.

Mackerel, jack
histological analysis 2
morphological analysis 2
offshore starvation 1
reproductive biology 841
starvation-induced mortality 1

Macrocytis pyrifera—see Kelp, giant

Macroinvertebrates
community studies in seagrass meadows 443

Macrouridae
abundance and distribution in Norfolk Canyon 35

Makalii—see Submersible

Mako, longfin—see Shark, longfin mako

MALLICOATE, DONNA L.—see PARRISH et al.

MALSBERGER, R. G.—see KEIRANS et al.

Manly-Parr
model for spawning escapement of chinook salmon .. 261

Mariana Archipelago
fishing experiment for caridean shrimp 927

Marine mammals
sizes of walleye pollock consumed 192

MASON, J. C., "Fecundity of the Pacific hake, *Merluccius productus*, spawning in Canadian waters" 209

MASON, J. C., and A. C. PHILLIPS, "An improved otter surface sampler" 480

MATSUURA, YASUNOBU, and NELSON TAKUMI YONEDA, "Early development of the lophiid anglerfish, *Lophius gastrophysus*" 429

McALICE, BERNARD, J.—see PODNIESINSKI and McALICE

McGOWAN, MICHAEL F., "Northern anchovy, *Engraulis mordax*, spawning in San Francisco Bay, California, 1978-79, relative to hydrography and zooplankton prey of adults and larvae" 879

Megaptera novaeangliae—see Whale, humpback

Menhaden, Atlantic
early life history 991

Menhaden, gulf
early life history 991
population and fishery characteristics 311

Merluccius productus—see Hake, Pacific

MERRINER, JOHN V.—see SMITH, JOSEPH W.

"Methodological problems in sampling commercial rockfish landings," by A. R. Sen 409

MEYERS, THEODORE R.—see HAWKES et al.

Micropogonius undulatus—see Croaker, Atlantic

MIDDLETON, ROBERT W., and JOHN A. MUSICK, "The abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfolk Canyon area" 35

MILNER, GEORGE B.—see RANCK et al.

"A model of the drift of northern anchovy, *Engraulis mordax*, larvae in the California Current," by James H. Power .. 585

"Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae," by Nancy C. H. Lo 395

Models
estimating food consumption of fish populations 827
Leslie 423
life-stage-specific instantaneous mortality rates 395
Manly-Parr 261

"Monitoring the sea surface chlorophyll concentration in the tropical Pacific: consequences of the 1982-83 El Niño," by Yves Dandonneau 687

MOONEY, ELIZABETH E.—see PEREZ and MOONEY

Morone saxatilis—see Bass, striped

"Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*," by Jill J. Grover and Bori L. Olla 484

"Morphology and possible swimming mode of a yellowfin tuna, *Thunnus albacares*, lacking one pectoral fin," by Jeffrey B. Graham, Richard H. Rosenblatt, and Darcy L. Gibson 463

"Movement of sea-run sea lampreys, *Petromyzon marinus*, during the spawning migration in the Connecticut River," by Kathleen Stier and Boyd Kynard 749

MOYLE, PETER B., ROBERT A. DANIELS, BRUCE HERBOLD, and DONALD M. BALTZ, "Patterns in distribution and abundance of a noncoevolved assemblage of estuarine fishes in California" 105

MUSICK, JOHN A.—see MIDDLETON and MUSICK

Mussel, blue
larvae in Damariscotta River estuary, Maine 995

Mya arenaria—see Clam, soft shell

MYRICK, A. C., JR., A. A. HOHN, J. BARLOW, and P. A. SLOAN, "Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific" .. 247

Mytilus edulis—see Mussel, blue

NELSON, WALTER R., and DEAN W. AHRENHOLZ, "Population and fishery characteristics of gulf menhaden, *Brevoortia patronus*" 311

Nematoscelis difficilis 157

Nereocystis leutkeana—see Kelp, bull

Netuma barba—see Catfish, sea

Neuston sampler
an improved otter surface sampler 480

New Bedford
ex-vessel price in New England fishing industry 437

New England
ex-vessel price in New England fishing industry 437

"New occurrence of epizootic sarcoma in Chesapeake Bay soft shell clams, *Mya arenaria*," by C. A. Farley, S. V. Otto, and C. L. Reinisch 851

Nezumia aequalis
abundance and distribution in Norfolk Canyon 35

Nezumia bairdii
abundance and distribution in Norfolk Canyon 35

NICHOLAS, JOHN R.—see PAYNE et al.

"Northern anchovy, *Engraulis mordax*, spawning in San Francisco Bay, California, 1978-79, relative to hydrography and zooplankton prey of adults and larvae," by Michael F. McGowan 879

Nursery studies
estuary studies 119

"Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus* in Chesapeake Bay," by Joseph W. Smith and John V. Merriner 871

O'BRIEN, LORETTA—see PAYNE et al.

"Occurrence of some parasites and a commensal in the American lobster, *Homarus americanus*, from the Mid-Atlantic Bight," by W. A. Van Engel, R. E. Harris, Jr., and D. E. Zwerner 197

OLLA, BORI L.—see GROVER and OLLA

Oncorhynchus gorbuscha—see Salmon, pink

Oncorhynchus kisutch—see Salmon, coho

Oncorhynchus nerka—see Salmon, sockeye

Oncorhynchus tshawytscha—see Salmon, chinook

Oregon
nursery areas for English sole 119

"Organic and trace metal levels in ocean quahog, *Arctica islandica* Linné, from the northwestern Atlantic," by Frank W. Steimle, Paul D. Boehm, Vincent S. Zdanowicz, and Ralph A. Bruno 133

Otoliths
age validation in Atlantic sailfish 493
catfish, sea 679
disposition rates 91
dolphin fishes in Hawaiian waters 186
increment technique for aging larval fishes 493

Otter surface sampler 480

OTTO, ROBERT S.—see SOMERTON and OTTO

OTTO, S. V.—see FARLEY et al.

OXENFORD, HAZEL A., and WAYNE HUNTE, "A preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus*, in the western central Atlantic" .. 451

Pacific eastern tropical
reproductive biology of the spotted dolphin 247

Pandalus borealis—see Shrimp, northern

Panulirus argus—see Lobster, spiny

Paralithodes platypus—see Crab, king

Parasite studies
American lobster 197
benthic amphipods infected with dinoflagellates 605
rhizocephalan infection in king crab 327
swordfish tapeworm 754

"Parasites of benthic amphipods: ciliates," by Phyllis T. Johnson 204

"Parasites of benthic amphipods: dinoflagellates (Duboscquodinida: Syndinidae)," by Phyllis T. Johnson 605

Parathemisto (hyperiid amphipod)
food items of Pacific salmon 77

Parophrys vetulus—see Sole, English

PARRISH, RICHARD H., DONNA L. MALLICOATE, and RICHARD A. KLINGBEIL, "Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*" 503

PARSONS, D. G., and G. E. TUCKER, "Fecundity of northern shrimp, *Pandalus borealis*, (Crustacea, Decapoda) in areas of the Northwest Atlantic" 549

PARSONS, GLENN—see KILLAM and PARSONS

"Patchiness and nutritional condition of zooplankton in the California Current," by Stewart W. Willason, John Favuzzi, and James L. Cox 157

"Patterns in distribution and abundance of a noncoevolved assemblage of estuarine fishes in California," by Peter B. Moyle, Robert A. Daniels, Bruce Herbold, and Donald M. Baltz 105

PAULY, DANIEL, "A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments" 827

PAYNE, P. MICHAEL, JOHN R. NICOLAS, LORETTA O'BRIEN, and KEVIN D. POWERS, "The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*" 271

PAYNE, P. MICHAEL—see SELZER et al.

PCB's
organic and trace metals in ocean quahog 133

PEARCY, W. G.—see KRYGIER and PEARCY

Penaeus aztecus—see Shrimp, brown

Penaeus setiferus—see Shrimp, white

PENNINGTON, MICHAEL, "Some statistical techniques for estimating abundance indices from trawl surveys".. 519

PEREZ, MICHAEL A., and MICHAEL A. BIGG, "Diet of northern fur seals, *Callorhinus ursinus*, off western North America" 957

PEREZ, MICHAEL A., and ELIZABETH E. MOONEY, "Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus*" 371

Petromyzon marinus—see Lampreys, sea

PHILLIPS, A. C.—see MASON and PHILLIPS

Phoca vitulina concolor—see Seal, harbor

PHONLOR, GERMANO—see POWELL and PHONLOR

Phytoplankton
zooplankton biomass and nutritional parameters..... 157

PIKITCH, ELLEN K.—see REXSTAD and PIKITCH

Plankton
identification of *Prionotus* 63

PODNIESINSKI, GREG S., and BERNARD J. McALICE, "Seasonality of blue mussel, *Mytilus edulis* L., larvae in the Damariscotta River estuary, Maine, 1969-77" 995

Pollock
ex-vessel price in New England fishing industry 437

Pollock, walleye
sizes consumed by marine mammals in the Bering Sea 192

Pollution
benthic animals as indicator species 133

POLOVINA, JEFFREY J., "A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock" 423

POLOVINA, JEFFREY J., and STEPHEN RALSTON, "An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas" 759

POP surveys
cetacean high-use habitats 345

"Population and fishery characteristics of gulf menhaden, *Brevoortia patronus*," by Walter R. Nelson and Dean W. Ahrenholz..... 311

Population sampling devices
shrimp trawls..... 981

Population studies
bass, black sea 723
dolphin 527
fish 535
menhaden, gulf 311
sardine 540

POTTHOFF, THOMAS, SHARON KELLEY, and JOAQUIN C. JAVECH, "Cartilage and bone development in scombroid fishes" 647

POWELL, ALLYN B., and GERMANO PHONLOR, "Early life history of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*" 991

POWER, JAMES H., "A model of the drift of northern anchovy, *Engraulis mordax*, larvae in the California Current" 585

POWERS, KEVIN D.—see PAYNE et al.

Predation
of northern anchovy 859

"A preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus*, in the western central Atlantic," by Hazel A. Oxenford and Wayne Hunte 451

PRESCOTT, ROBERT—see SELZER et al.

PRINCE, ERIC D., DENNIS W. LEE, CHARLES A. WILSON, and JOHN M. DEAN, "Longevity and age validation of a tag-recaptured Atlantic sailfish, *Istiophorus platypterus*, using dorsal spines and otoliths" 493

Prionotus carolinus—see Searobin, northern

Prionotus evolans—see Searobin, striped

Quahog, ocean
organic and trace metal levels 133

QUAST, JAY C., "Annual production of eviscerated body weight, fat, and gonads by Pacific herring, *Clupea harengus pallasi*, near Auke Bay, southeastern Alaska" 705

RALSTON, STEPHEN—see DAILEY and RALSTON
—see POLOVINA and RALSTON

RALSTON, STEPHEN, "An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Marina Archipelago" 927

RALSTON, STEPHEN, REGINALD M. GOODING, and GERALD M. LUDWIG, "An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll" 141

RANCK, CAROL L., FRED M. UTTER, GEORGE B. MILNER, and GARY B. SMITH, "Genetic confirmation of specific distinction of arrowtooth flounder, *Atheresthes stomias*, and Kamchatka flounder, *A. evermanni*" 222

"Rates of increase in dolphin population size," by Stephen B. Reilly and Jay Barlow 527

RATTY, F. J., Y. C. SONG, and R. M. LAURS, "Chromosomal analysis of albacore, *Thunnus alalunga*, and yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*, tuna" 469

Ray, cownose
reproductive biology 871

Red tide
effects on *Gymnodinium splendens* swimming speed 460

REINISCH, C. L.—see FARLEY et al.

REILLY, STEPHEN B., and JAY BARLOW, "Rates of increase in dolphin population size" 527

REIS, ENIR GIRONDI, "Age and growth of the marine catfish, *Netuma barba* (Siluriformes, Ariidae), in the estuary of the Patos Lagoon (Brasil)" 679

RENAUD, MAURICE L., "Hypoxia in Louisiana coastal waters during 1983: implications for fisheries" 19

"Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific," by A. C. Myrick, Jr., A. A. Hohn, J. Barlow, and P. A. Sloan 247

"Reproductive biology of king mackerel, *Scomberomorus cavalla*, from the southeastern United States," by John H. Finucane, L. Alan Collins, Harold A. Brusher, and Carl H. Saloman 841

Reproductive studies
anchovy, northern 503, 879
bass, black sea 723
crab, golden king 571
dolphin, spotted 247
mackerel, king 841
mussel, blue 995
ray, cownose 871
shrimp, caridean 915
squid, market 771
tuna, skipjack 895

"Resilience of the fish assemblage in New England tidepools," by Bruce B. Collette 200

Resource assessment techniques
hydroacoustic echo integration 287
line intercept survey 287
line transect survey 287
abundance of widow rockfish 287

REXSTAD, ERIC A., and ELLEN K. PIKITCH, "Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*" 947

Rhinoptera loonasus—see Ray, cownose

"Rhizocephalan infection in blue king crabs, *Paralithodes platypus*, from Olga Bay, Kodiak Island, Alaska," by P. T. Johnson, R. A. MacIntosh, and D. A. Somerton 177

Rhizocephalans
length-weight relationships of king crab 327

Rockfish
problems in sampling commercial landings 409

Rockfish, widow
behavior studies 287
methodologies for assessing abundance 287

Rockfish, yellowtail
fat volume comparisons 743

ROGERS, S. GORDON, HIRAM T. LANGSTON, and TIMOTHY E. TARGETT, "Anatomical trauma to sponge-coral reef fishes captured by trawling and angling" ... 697

"The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon," by E. E. Krygier and W. G. Pearcy 119

ROSENBLATT, RICHARD H.—see GRAHAM et al.

ROUMILLAT, WILLIAM A.—see WENNER et al.

Sablefish, larval
starvation 484
prey size selection 484

Sailfish, Atlantic
longevity and age validation 493

Salmon, chinook
methods used to estimate spawning escapement..... 261

Salmon, Pacific
food habits in the Strait of Juan de Fuca 77

Salmon, smolts
correlation with seabirds 279

SALOMAN, CARL H.—see FINUCANE et al.

Samplers
improved otter surface sampler..... 480

Sarcoma
occurrence in soft shell clams 851

Sardine
population collapse 535
population studies 535

"Scavenger feeding by subadult striped bass, *Morone saxatilis*, below a low-head hydroelectric dam," by John Warner and Boyd Kynard 220

Scomberomorus cavalla—see Mackerel, king

Scombroid fish
cartilage and bone development 647

Sea surface studies
monitoring chlorophyll concentration in the tropical Pacific 687

Seabirds
correlations with salmon smolts..... 279

"Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Niño," by Range D. Bayer.. 279

Seagrass meadows
community studies..... 443
comparison of two sampling methods 443

Seal, harbor
in southern New England..... 217

Seal, northern fur
arrival times and numbers on St. Paul Island, Alaska.. 383
diet 957
food and energy consumption of lactating females ... 371

Searobin, northern
differentiation of *Prionotus* eggs 63

Searobin, striped
differentiation of *Prionotus* eggs 63

"Seasonality of blue mussel, *Mytilus edulis* L., larvae in the Damariscotta River estuary, Maine, 1969-77," by Greg S. Podniesinski and Bernard J. McAlice 995

Sebastes entomelas—see Rockfish, widow

Sebastes flavidus—see Rockfish, yellowtail

SELZER, LAWRENCE, A., GREG EARLY, PATRICIA M. FIORELLI, P. MICHAEL PAYNE, and ROBERT PRESCOTT, "Stranded animals as indicators of prey utilization by harbor seals, *Phoca vitulina concolor*, in southern New England" 217

SEN, A. R., "Methodological problems in sampling commercial rockfish landings" 409

"The sex ratio and gonad indices of swordfish, *Xiphias gladius*, caught off the coast of Southern California in 1978," by Earl C. Weber and Stephen R. Goldberg ... 185

Shark, longfin mako
first record in the Gulf of Mexico 748

SHEPARD, ANDREW N., ROGER B. THEROUX, RICHARD A. COOPER, and JOSEPH R. UZMANN, "Ecology of Ceriantharia (Coelenterata, Anthozoa) of the northwest Atlantic from Cape Hatteras to Nova Scotia".. 625

SHIRLEY, THOMAS C.—see HAWKES et al.

Shrimp
affect of hypoxia on abundance and distribution..... 19

Shrimp, caridean
an intensive fishing experiment..... 927
reproduction, distribution, and growth 915

Shrimp, northern
fecundity studies in northwest Atlantic 549

Shrimp, penaid
population sampling..... 981

Shrimp, pink—see Shrimp, northern

SIBERT, JOHN R.—see HUNTER et al.

"A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments," by Daniel Pauly 827

"Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea," by Kathryn J. Frost and Lloyd F. Lowry 192

"Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes," by Arild Folkvord and John R. Hunter 859

SLOAN, P. A.—see MYRICK et al.

SMITH, GARY B.—see RANCK et al.

SMITH, JOSEPH, W., and JOHN V. MERRINER, "Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay" 87

SMITH, T. D.—see LO and SMITH

Snappers
yield assessment in the Marianas 759

Sole, English
estuarine and offshore nursery areas 119

SOMERTON, D. A.—see JOHNSON et al.

SOMERTON, DAVID A., and ROBERT S. OTTO, "Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the eastern Bering Sea" 571

"Some statistical techniques for estimating abundance indices from trawl surveys," by Michael Pennington 519

SONG, Y. C.—see RATTY et al.

SORENSEN, PETER W., MARCO L. BIANCHINI, and HOWARD E. WINN, "Diel foraging activity of American eels, *Anguilla rostrata* (LeSueur), in a Rhode Island estuary" 746

"Sounds from Bryde, *Balaenoptera edeni*, and finback, *B. physalus*, whales in the Gulf of California," by William C. Cummings, Paul O. Thompson, and Samuel J. Ha 359

Southern California Bight
distribution and abundance of common dolphin 333

Squid, market
growth, behavior, and sexual maturation 771

SQUIRES, DALE, "Ex-vessel price linkages in the New England fishing industry" 437

"The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific," by J. Roe Hunter, Beverly J. Macewicz, and John R. Sibert 895

"Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods," by Gail H. Theilacker 1

Statistical methods
estimating abundance 519

STEIMLE, FRANK W., PAUL D. BOEHM, VINCENT S. ZDANOWICZ, and RALPH A. BRUNO, "Organic and trace metal levels in ocean quahog, *Arctica islandica* Linné, from the northwestern Atlantic" 133

Stenella attenuata—see Dolphin, spotted

STEPIEN, CAROL A., "Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard, 1854" 809

STIER, KATHLEEN, and BOYD KYNARD, "Abundance, size, and sex ratio of adult sea-run sea lampreys, *Petromyzon marinus*, in the Connecticut River" 476

STIER, KATHLEEN, and BOYD KYNARD, "Movement of sea-run sea lampreys, *Petromyzon marinus*, during the spawning migration in the Connecticut River" 749

"Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*," by Eric A. Rexstad and Ellen K. Pikitch 947

"Stranded animals as indicators of prey utilization by harbor seals, *Phoca vitulina concolor*, in southern New England," by Lawrence A. Selzer, Greg Early, Patricia M. Fiorelli, P. Michael Payne, and Robert Prescott 217

Submersibles
resource assessment at Johnston Atoll 141

"Survival and growth of striped bass, *Morone saxatilis*, and *Morone* hybrid larvae: laboratory and pond enclosure experiments," by Edward D. Houde and Lawrence Lubbers III 905

Swordfish
sex ratio and gonad indices 185
morphology of *Fistulicola plicatus* 754

SYKES, STEPHEN D., and LOUIS W. BOTSFORD, "Chinook salmon, *Oncorhynchus tshawytscha*, spawning escapement based on multiple mark-recapture of carcasses" 261

TARGETT, TIMOTHY E.—see ROGERS et al.

Taxonomy
arrowtooth and Kamchatka flounders 222

TESTER, PATRICIA A., and ANDREW G. CAREY, JR., "Instar identification and life history aspects of juvenile deepwater spider crabs, *Chionoecetes tanneri* Rathbun" 973

THEILACKER, GAIL H., "Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods" 1

Theragra chalcogramma—see Pollock, walleye

THEROUX, ROGER B.—see SHEPARD et al.

THOMPSON, PAUL O.—see CUMMINGS et al.

Thunnus alalunga—see Albacore

Thunnus albacares—see Tuna, yellowfin

Tidepools
fish assemblages in New England 200

Townsend Cromwell
resource assessment at Johnston Atoll 141

Trachurus symmetricus—see Mackerel, jack

Trawls, shrimp
population sampling devices 981

Trawl surveys
statistical methods for estimating abundance 519

Trawling
anatomical trauma to sponge-coral reef fishes 697

TUCKER, G. E.—see PARSONS and TUCKER

Tuna, skipjack
chromosomal analysis 469
spawning frequency 895

Tuna, yellowfin
chromosomal analysis 469
incidental dolphin mortality 559
morphology and swimming mode 463

TURK, P. E.—see YANG et al.

"Type, quantity, and size of food of Pacific salmon (*Oncorhynchus*) in the Strait of Juan de Fuca, British Columbia," by Terry D. Beacham 77

UCHIYAMA, JAMES H., RAYMOND K. BURCH, and SYD A. KRAUL, JR., "Growth of dolphins, *Coryphaena hippurus* and *C. equiselis*, in Hawaiian waters as determined by daily increments on otoliths" 186

Underwater sounds
Bryde and finback whales 359

UTTER, FRED M.—see RANCK et al.

UZMANN, JOSEPH R.—see SHEPARD et al.

VAN ENGEL, W. A., R. E. HARRIS, JR., and D. E. ZWERNER, "Occurrence of some parasites and a commensal in the American lobster, *Homarus americanus*, from the Mid-Atlantic Bight" 197

"A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock," by Jeffrey J. Polovina 423

"Variations in the morphology of *Fistulicola plicatus* Rudolphi (1802) (Cestoda: Pseudophyllidea) from the swordfish, *Xiphias gladius* L., in the northwest Atlantic Ocean," by W. E. Hogans and P. C. F. Hurley 754

WAHLEN, BRUCE E., "Incidental dolphin mortality in the eastern tropical Pacific tuna fishery, 1973 through 1978" 559

WALTZ, C. WAYNE—see WENNER et al.

WARNER, JOHN, and BOYD KYNARD, "Scavenger feeding by subadult striped bass, *Morone saxatilis*, below a low-head hydroelectric dam" 220

WEBER, EARL C., and STEPHEN R. GOLDBERG, "The sex ratio and gonad indices of swordfish, *Xiphias gladius*, caught off the coast of Southern California in 1978" 185

WENNER, CHARLES A., WILLIAM A. ROUMILLAT, and C. WAYNE WALTZ, "Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States" 723

Whales, Bryde
underwater sounds in the Gulf of California 359

Whales, finback
underwater sounds in the Gulf of California 359

Whales, humpback
distribution in relation to sand eels 271

WILKINS, MARK E., "Development and evaluation of methodologies for assessing and monitoring the abundance of widow rockfish, *Sebastes entomelas*" 287

WILLASON, STEWART W., JOHN FAVUZZI, and JAMES L. COX, "Patchiness and nutritional condition of zooplankton in the California Current" 157

WILSON, CHARLES, A.—see PRINCE et al.

WINN, HOWARD E.—see KENNEY and WINN
—see SORENSEN et al.

Xiphias gladius—see Swordfish

YANG, M. S., and P. A. LIVINGSTON, "Food habits and diet overlap of two congeneric species, *Atheresthes stomias* and *Atheresthes evermanni*, in the eastern Bering Sea" 615

YONEDA, NELSON TAKUMI—see MATSUURA and YONEDA

ZDANOWICZ, VINCENT S.—see STEIMLE et al.

Zooplankton
California Current 157

ZWERNER, D. E.—see VAN ENGEL et al.

NOTICES

NOAA Technical Reports NMFS published during first 6 months of 1986.

39. Survey of fish protective facilities at water withdrawl sites on the Snake and Columbia Rivers. By George A. Swan, Tommy G. Withrow, and Donn L. Park. April 1986, iii + 34 p., 26 figs., 6 tables.

Some NOAA publications are available by purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

Gulf of Mexico Ichthyoplankton Samples

The **Gulf States Marine Fisheries Commission** wishes to announce the availability of Gulf of Mexico ichthyoplankton samples for loan to qualified researchers. Samples have been and are continuing to be collected for SEAMAP (Southeast Area Monitoring and Assessment Program), a multi-year international federal/state/university program of the GSMFC. Neuston and bongo nets were employed for specimen collection in a one degree latitude/longitude grid over the entire Gulf from 26°N northward and sorted and preliminarily identified by the Plankton Sorting and Identification Center, Szczecin, Poland. At present samples from 1982 (7057 lots, 93 families), 1983 (8351 lots, 106 families) and material from one summer cruise in 1984 (4155 lots, 75 families) are available for loan. Lots of unsorted fish eggs are also available from these years. Most samples are sorted to the family level, although many have identification to generic or species level. Additional 1984 samples are expected to become available by the end of 1986. Specimens are available for loan on a 6-month renewable basis. Researchers interested in obtaining additional information can contact either SEAMAP Ichthyoplankton Curator, Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg, FL 33701, or SEAMAP Coordinator, Gulf States Marine Fisheries Commission, P.O. Box 726, Ocean Springs, MS 39564.

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The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 12, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Fourth Edition, 1980.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on high quality or glossy paper.

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Common **abbreviations** and **symbols,** such as mm, m, g, L, mL, mg, °C (for Celsius), %, ‰, and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

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Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

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REXSTAD, ERIC A., and ELLEN K. PIKITCH. Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus* 947
PEREZ, MICHAEL A., and MICHAEL A. BIGG. Diet of northern fur seals, *Callorhinus ursinus*, off western North America 957
TESTER, PATRICIA A., and ANDREW G. CAREY, JR. Instar identification and life history aspects of juvenile deepwater spider crabs, *Chionoecetes tanneri* Rathbun ... 973

Notes

CODY, TERRY J., and BILLY E. FULS. Comparison of catches in 4.3 m and 12.2 m shrimp trawls in the Gulf of Mexico 981
POWELL, ALLYN B., and GERMANO PHONLOR. Early life history of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus* 991
PODNIESINSKI, GREG S., and BERNARD J. McALICE. Seasonality of blue mussel, *Mytilus edulis* L., larvae in the Damariscotta River estuary, Maine, 1969-77 995

Index 1003

Notices 1017

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